ANALYSIS OF FRESHWATER INFLOW EFFECTS ON METABOLIC STRESSES OF SOUTH TEXAS BAY AND ESTUARINE FISHES: RATES OF ADAPTABILITY TO CHANGING SALINITY-TEMPERATURE REGIMES

Draft Final Report to:
Texas Department of Water Resources
Interagency Cooperation Contract
No. IAC (78-79)-1840
TDWR Contract No. 14-90019

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January 8, 1980

Texas Department of Water Resources
1700 N. Congress Avenue
P. O. Box 13087 Capitol Station
Austin, Texas 78711

Attention: Dr. Herbert W. Grubb
Mr. Gary L. Powell

Gentlemen:

The accompanying report is submitted with great pleasure. It is "ANALYSIS OF FRESHWATER INFLOW EFFECTS ON METABOLIC STRESSES OF SOUTH TEXAS BAY AND ESTUARINE FISHES: RATES OF ADAPTABILITY TO SALINITY-TEMPERATURE REGIMES." The support was under IAC (78-79)-1840, TDWR Contract No. 14-90019. We send our sincere thanks for this support.

The report is almost entirely based on the M.A. thesis, "STUDIES ON THE TIME COURSE OF ACCLIMATION TO SALINITY CHANGES IN JUVENILE SPOTTED SEATROUT AND RED DRUM," which has been submitted to the University of Texas Graduate School by Mr. Michael P. Gunter. The numbering of the tables and figures in the report follows that of Gunter's thesis. In addition to Mike Gunter, special acknowledgements are due to Ron Ilg, who helped initiate work on the small fish earlier and who is continuing work with them for his Ph.D. dissertation. Throughout these investigations on the south Texas estuarine fishes, the general perspective and advice afforded by Mr. Gary Powell and other TDWR personnel have been highly valued. The initial TDWR investigations have thus opened up a number of very promising and practical research avenues.

Apologies for the lateness of this report are due solely to the principal investigator's unavoidable 1-1/2 year delay in completing the previous report. The forebearance of TDWR in this matter is greatly appreciated.

Again, we all emphasize our gratitude for the TDWR support during the past several years.

Respectfully submitted,

Donald E. Wohlschlag

Donald E. Wohlschlag
Principal Investigator

Professor of Zoology and
Marine Studies

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FINAL REPORT

TO

TEXAS DEPARTMENT OF WATER RESOURCES

for

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ANALYSIS OF FRESHWATER INFLOW EFFECTS ON METABOLIC STRESSES OF SOUTH TEXAS BAY AND ESTUARINE FISHES: RATES OF ADAPTABILITY TO CHANGING SALINITY-TEMPERATURE REGIMES

Principal Investigator:

Donald E. Wohlschlag

Research Assistants:

Ronald J. Ilg

Michael P. Gunter

The University of Texas at Austin
Marine Science Institute
Port Aransas Marine Laboratory
Port Aransas, Texas 78373

UT Account No. [redacted]

EXECUTIVE SUMMARY---RECOMMENDATIONS

The purpose of these experiments with juvenile spotted seatrout and red drum is to establish a methodology of assessing the ability of fish acclimated to estuarine salinity levels to withstand short term stresses of increased or decreased salinity at winter 15°C and summer 28°C temperatures.

The experiments were conducted by determining the metabolic performance of the fish acclimated to 20 ppt salinity, which is near optimum, and then subjecting the fish to salinities of 10, 30 or 40 ppt salinity in order to follow their reactions and propensities to recover and readjust to the new salinity levels. For the red drum only a similar experiment was carried out except that the blood serum osmolality (as a measure of the degree of adaptability) was followed. For both kinds of experiments, the time course was followed by measuring at frequent intervals the metabolic or the blood osmolality levels for three-day periods.

Metabolic performance was measured as the scope for activity, which is the difference between the respiratory metabolism at maximum sustained activity and at the lowest maintenance (standard) level.

During the first hour or so the <u>reaction phase</u> to a salinity change usually was accompanied by an abrupt drop in the scope, followed by a variously extended low metabolic level <u>stressed phase</u> and then by a rising <u>recovery phase</u> at about 30 hours. By about 48 hours typically there was reasonable

stabilization phase, when scope was lowered, principally by reduction in the active metabolic level and very little influenced by a change in standard level.

For the first three hours after a salinity change, the smaller the fish the greater was the decrease in metabolic scope. The greater the salinity change the greater the duration of the stressed phase and the length of time for the initiation of recovery phase.

Temperature is relatively not important except at the upper (28°C) levels for the small fish, and possible at salinity extremes of 10 and 40 ppt for the red drum at both 28°C and 15°C where the active metabolic rates are about equal.

In general, the sudden temporary stresses caused by salinity changes are more severe than the steady state stresses at salinities far from optimum. However, this study indicates that it is possible to utilize the rapid salinity change technique with small fish to assess their capabilities to become acclimatized to salinity changes. It would appear that rapid changes toward lower salinities, which also can occur rapidly in nature, result in less stress than rapid changes to progressively higher salinities, which ordinarily occur only slowly in nature. Rapid changes to higher salinities are also accompanied by osmolarity malfunctions in regulation and death in contrast to rapid changes to lower salinities that do not usually result in osmoregulatory problems and death. With the various cautions discussed in the study, it appears that young fish do respond to rapid salinity changes in a way that is

indicative of similar, but slower, responses in the natural estuaries. Therefore it would appear reasonable to suppose that the methods of this study could be developed further for different species, different size ranges, seasons, and other variables in relation to anticipated salinity changes.

INTRODUCTION

NOTE--

The materials in this report are taken directly from a Master's Thesis presented December 1979 by Mr. Michael Preston Gunter to the Faculty of the Graduate School of The University of Texas at Austin in partial fulfillment of the requirements for the degree of Master of Arts. The thesis title is: "Studies on the Time Course of Acclimation to Salinity Changes in Juvenile Spotted Seatrout and Red Drum." The numbering of the figures and tables follows Gunter's thesis, which is largely paraphrased or quoted throughout.

The purpose of this study is to characterize the rates of adaptability to salinity-temperature regimes by small red drum (Sciaenops ocellata) and spotted seatrout (Cynoscion nebulosus), with particular reference to rates, or relative rates, of acclimatization to changing salinity gradients.

Both species are important commercially and recreationally, and both are generally euryhaline (Gunter, 1945), although the red drum probably spawn in the Gulf just outside passes (Simmons and Breuer, 1962). Earlier work on adults and subadults indicates that the optimal metabolic scope-salinity relationship is near 20 ppt (Wohlschlag and Wakeman, 1978; Wohlschlag, 1977). Especially beyond 30 ppt, these authors have shown that the metabolic scope and swimming performances drop rapidly.

Kinne (1962) has noted that salinity at spawning times may cause permanent nongenetic changes in morphology, growth rate, salinity tolerance, and metabolic responses. Kinne (1964) also notes that salinity per se influences the solubility of oxygen, the ammonia to ammonium ion ratios, and the densities and viscosities. However, as Bern (1975) notes, from about 10 to 48 times the body area is gill surface, which is the immediate surface of response to salinity changes or regimes.

The ionic and osmoregulatory problems of estuarine fishes are well known, but the variety of mechanisms and influencing circumstances are not always well understood. Conte (1969) reviews the marine teleost system of swallowing water and secreting accumulated salts at the gills or kidney. Urine flow in marine teleosts is inadequate for water balance maintenance, and according to Maetz (1974), Parry (1966), among others, most salt excretion is extrarenal.

Particularly important are the so-called "chloride secretory cells" in the gills (Conte, 1969; Parry, 1965; Gordon, 1964). Gill permeability is largely endocrine-controlled by hormones like prolactin (Sage, 1973; Sage and DeVlaming, 1975; Johnson, et al., 1974), cortisol (Bern, 1975), and epinephrine (Isaia, 1979).

Maetz (1974) has summarized much of the research on high and low salinity adaptations by marine teleosts. Motais, et al. (1966) indicate that there are two types of euryhalinity: (1) by control of plasma osmotic concentrations, and (2) by a

tolerance of variation in plasma ion concentration or "cellular resistance" as in Fundulus spp.

Temperature also influences salinity effects. Kirsch (1972) associated increase in temperature with urinary water and electrolyte excretion for the eel, while Mackay (1974) noted that at both upper and lower incipient lethal temperatures plasma sodium and chloride concentrations decreased. At a lower temperatures, at least, these lower concentrations may reduce ionic and osmotic regulatory energy requirements.

The relationship of temperature and salinity has been studied extensively by Kinne (1964) for a euryhaline cyprinodont fish, whose optimal growth occurred at optimal temperature of 25°C in both fresh and sea water. Brett (1976) has shown that the optimum scope for activity and optimum growth rate for the sockeye salmon, while different conceptually, both occur at 15°C.

Relationships between routine oxygen consumption rates and salinity have been compiled by Nordlie (1978), who noted that there are four general patterns depending upon degree of metabolic response to salinity and upon relation of metabolic response to the serum isosmotic level. Wohlschlag and Wakeman (1978) noted that the spotted seatrout adults and subadults had minimal (standard) levels and maximal active levels, and accordingly the maximum scope, somewhat above the isosmotic level.

The energy costs of osmoregulation are variously estimated or measured. Potts (1954) indicated that theoretically at least the costs are quite small and may be easily masked by other

factors. Rao (1968) had measurements to indicate that osmoregulation was as high as 27% of all energy costs in terms of oxygen consumption; Farmer and Beamish (1969), as high as 29%.

The interpretation that osmoregulatory costs of Rao's (1968) trout can be added to the scope was suggested by Fry (1971) since Rao found that at all swimming velocities observed the metabolic rate was always minimal near the isosmotic level (7.5 ppt), but only up to a salinity of about 15 ppt after which metabolic costs increased relatively more for smaller fish. Similar studies on mullet by Nordlie and Leffler (1975) and Collins (1974) indicate also that lowest standard rates are near the isosmotic points and standard rates tend to increase both above and below 10-11 ppt until maintenance costs are about doubled at 45 ppt.

Oxygen consumption at all velocities was lowest at the isosmotic salinity of 11.6 ppt for the Tilapia nilotica studied by Farmer and Beamish (1969), who also found that exercised fish were less capable of maintaining constant plasma osmotic concentrations than were unexercised fish. With a possible competition for energy allocation between ion-osmotic regulation and swimming, it is expected that the swimming velocities would have to decline when salinities departed widely from those near isosmoticity (Wohlschlag and Wakeman, 1978), or altered blood osmolarities as in Tilapia (Rao, 1968; Fry, 1971). Interspecific comparisons among fishes are difficult, whether their affinities

are freshwater, estuarine or marine, whether their life history operational modes are resident, anadromous, or catadromous, all may have quite widely different relationships to salinity, even though all might be determined to be euryhaline.

However diverse the salinity relationships may be to activity as was growth, and metabolism in general, ion-osmoregulation appears to be contolled by endocrines, particularly prolactin and cortisol, and influenced by such environmental factors as temperature. At the present time, the great diversity of literature on these subjects does not seem to provide any clear cut guidelines for predicting what happens when a particular species at a particular size or age range is subjected to a particular salinity regime. More specifically, little is known about the time course of fish adaptations to salinity changes.

Ventkataramiah, et al. (1977) in their studies of the time course of brown shrimp adaptation to salinity changes found that metabolic and osmotic adaptation occurred faster at 25°C than at 18°C or 32°C. Three adaptation phases were: (1) immediate responses, (2) stabilization, and (3) new steady state levels. They found that there was a positive interaction of metabolic and osmotic responses at 25°C, but the interaction was inconsistent at more extreme temperatures. Temperature changes affected each ion independently, although ion regulation appeared to be generally temperature-dependent. Smaller shrimp appeared to prefer higher salinities and lower temperatures. Thus, the detailed study with the shrimp, appeared to have much in common

with local studies on the red drum, spotted seatrout, and other species in that spawning, hatching, developmental patterns, and subsequent life history stages would be normally suspected of eliciting different metabolic and metabolism-related responses depending upon salinity.

METHODS AND MATERIALS

Sources of Fish--Acclimatization

From September 1978 through August 1979 small red drum and spotted seatrout were captured either by seine or otter trawl in the vicinity of Port Aransas, Texas. Most individuals were taken from seagrass beds near Marker 85 in the Lydia Ann Channel. Small (1-2 g) red drum were also obtained from the Texas Parks and Wildlife Department redfish rearing ponds at Palacios, Texas, which permitted the use of small fish at 28°C, which would not have been possible otherwise, due to the fact that underyearlings during the summer in the field are in the 50-100 g weight range. After capture, fish were placed in thermally controlled holding tanks at the experimental temperature (15 or 28°C) and at 20 ppt salinity and held for at least three days. These fish were fasted the day before insertion into the respirometers, and oxygen consumption measurements were not performed until the following day.

General Procedures

Three physiological variables were monitored over a 72-hour period following salinity changes. These variables are:

Active Metabolic Rate--the rate of oxygen consumption at given temperatures and salinities for a fasted fish swimming at its maximum sustained swimming speed.

Resting Metabolic Rate--the rate of oxygen consumption at given temperatures and salinities of a fasted fish confined to a respiration chamber and shielded as much as possible from exogenous stimuli, e.g., light, noise, etc.

Whole Blood Osmolality--mOsm/kg--a measure of the osmotic pressure exerted by the blood as measured by the colligative properties, e.g., vapor pressure, which change as a result of solute activity in the blood. Since vapor pressure depression is the variable measured here, the erythrocytes have no effect on the measurement. (This variable was measured only for small red drum.)

These variables were measured one hour before the salinity changes and at 1, 3, 6, 12, 24, 30, 48, 54, and 72 hours after the change, except for the 20-40 ppt change in which the 1-hour reading was necessarily omitted. Salinity changes studied were from 20 ppt to 10, 30, or 40 ppt. Responses to these changes were studied under winter (15°C) and summer (28°C) conditions.

Each experimental run consisted ideally of one determination of the active metabolic rate, four determinations of resting metabolic rate, and as many determinations of whole blood osmolality as could be made with the number of fish on hand, usually 2-3, at each time interval. When the experimental fish (especially small red drum) lost weight during the 72 hour "run",

weights were measured before and after the "run". Linear weight loss over time was assumed, and interpolated values were used in metabolic rate determinations.

Metabolic Rate Measurements

Active Metabolic Rate--This variable was measured using the Wohlschlag modified Blazka respirometer, which has been described previously (Wohlschlag and Wakeman, 1978). Due to the generally small size of the juvenile fishes studied, a group (school) of fish of similar size were run simultaneously in the apparatus. They were inserted into the chambers about 15 hours before the salinity change and allowed to adjust to the chamber overnight before any oxygen consumption readings were taken. The respirometer is fully temperature controlled ($\pm$ 1°C). Aeration during this period was provided by the flow through system described below. Oxygen consumption at maximum sustained swimming speed was measured as the decrease in the partial pressure of oxygen (pO_2) during an interval of about 60 min. The pO_2 decrease was converted to mgO_2/hr^{-1} allowing for the duration of the time interval, the oxygen solubility coefficient (Green and Carrit, 1967) at the appropriate salinity and temperature, the volume of the chamber (207 l), and appropriate $p^0{}_2$ to mgO_2 conversion factors. The pO_2 of the water in the chamber was measured by injecting samples into a Radiometer E5047 oxygen electrode connected to a Radiometer PHM-71 acid-base analyzer with a PHA930 pO_2 module.

Following a 15-20 min. "warm-up" period the speed of the

water flow in the chamber was increased by increments until the relative steady propulsive swimming wave of the fish began to show severe tail beat frequency aberrations commonly known as a shift to 'burst and glide" swimming. Experience has shown that just below this speed is the maximum sustained swimming speed, or that which can be powered aerobically for 100-200 min. (Webb, 1975). This level was determined for each time interval and is the level at which the active metabolic rate was measured. Because of the small size and the number of fish in the Blazka chamber, the maximum sustained velocity could be slightly underestimated (see Discussion).

Resting Metabolic Rate--To measure this rate, one to three fish were inserted into darkened 2.9 l Fernbach flasks immersed in a constant temperature water bath. These flasks were equipped with syringe ports in the stoppers and polyethylene tubing running to the central volume of the flask. A small bleed hole in the stopper allowed water displacement when 3 ml samples were taken. Oxygen consumption measurement was performed in the manner described above, and at essentially the same time as the active metabolic rate. Aeration between readings was accomplished by removing the stoppers, and covering the tops of the flasks with netting. Convection, aided by airstones, in the water bath, provided mixing and aeration.

Blood Osmolality

Blood osmolality was measured with a Wescor 5130B vapor pressure osmometer which requires only enough blood to saturate a 6 mm diameter filter paper disc. Due to the small size of

fish involved, a special technique for vampirizing them was developed. Individuals were removed from their holding container, rinsed with deionized water, and blotted dry. The tail was then severed posterior to the anus with a scalpel. The anterior cross section was then blotted once to avoid contamination with intracellular fluid and the blood issuing from the caudal artery was soaked up by a small filter paper disc which was immediately placed in the osmometer. To facilitate bleeding, very small fish were spun at arms length for a few seconds to let centrifugal force take blood to the posterior end of the fish. This entire procedure took less than one minute.

Salinity Changes

All salinity changes occurred at the same rate of approximately 10 ppt hr^{-1}. This was accomplished by the use of a 126 l salinity change reservoir and a pump with tubing to carry flow into the Blazka chamber (see Fig. 1). A return hose carried water back to the reservoir. By starting at a predetermined salinity in the reservoir, the pump could be turned on causing water in the reservoir to cycle with the water in the chamber. Equilibrium at the test salinity was reached in 50-60 min. For the changes from 20 to 40 ppt, the salinity change occurred in two phases, the first from 20 to 30 ppt and the second from 30 to 40 ppt. This procedure took 100-120 min.

The running sea water of the lab was used in all experiments.

Figure 1. Diagram of the 207 l modified Blazka respirometer.

M --variable speed motor

I --impeller

PS--posterior screen

ST--transparent acrylic swimming tunnel

B --flow linearizing baffles

CT--constant temperature water bath

ET--circular exercise tank

SR--salinity change reservoir

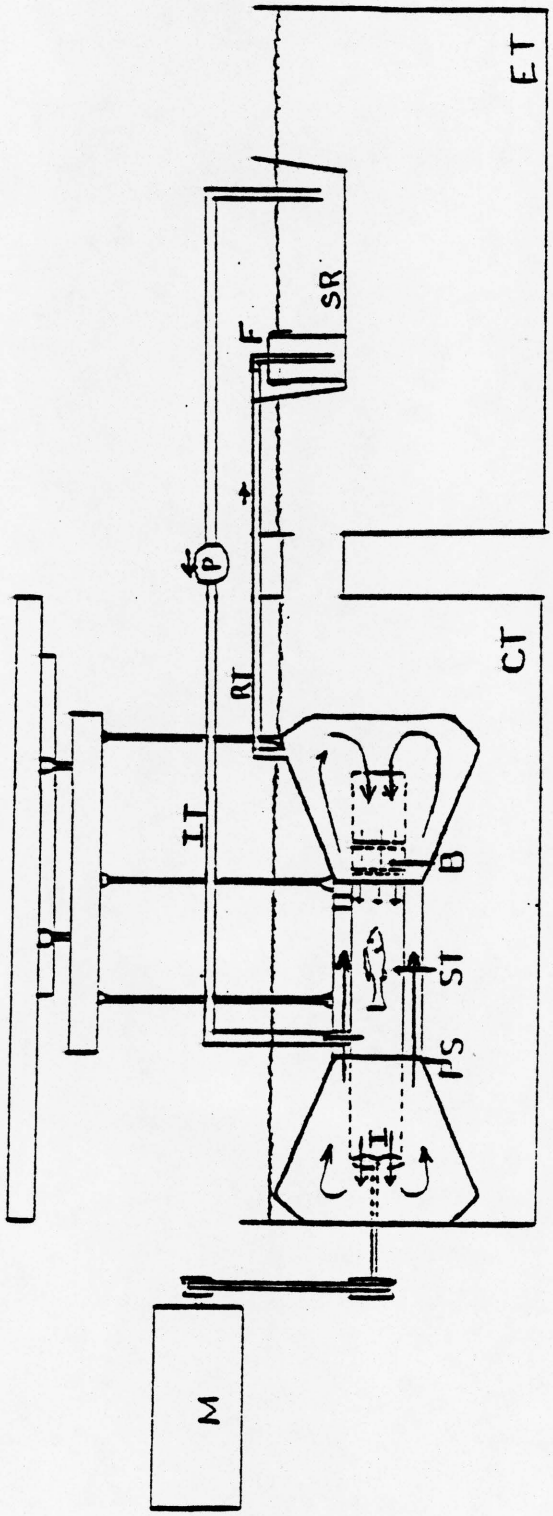
F --filter

P --pump

IT--inflow tubing

RT--return tubing

(Adapted from Wakeman and Wohlschlag, 1978)


ET
SR
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M

Salinities were adjusted by either dilution with deionized water or by adding commercial sea salts.

Calculations

Underyearlings used in this study ranged in weight from 1 to 147 g. Because size is a critical factor governing the metabolic rate, a procedure to standardize all data for weight was needed. Further, activity (swimming speed) is very important as a controlling factor and although each active metabolic rate measurement was at the determined sustained velocity, there was variation in the number of lengths per second the groups attained. To achieve standardization of the data and to evaluate the effect of the salinity change alone, a series of multiple regression analyses were performed using log average weight (log $\overline{WT}$) and average total lengths per second ($\overline{TL}$ s^{-1}) as independent variables and log $mg0_2kg^{-1}hr^{-1}$ (Y kg^{-1}) as the dependent variable. The regressions then take the form:

$$\hat{Y} = a + b_w X_w + b_v X_v$$

where: $\hat{Y}$ = log $mg0_2hr^{-1}$

a = a constant

b_w = partial correlation coefficient of average body wet weight

b_v = partial correlation coefficient of velocity in average total lengths per second (TL s^{-1})

X_w = log average weight (g)

X_v = velocity in TL s^{-1}

This procedure was conducted for each species at each temperature.

(See Tables 1 and 2 with relevant statistics in Tables 3 and 4 in the next section.) Data selected for these regressions came from previous studies in this laboratory (Wakeman, 1978; Wohlschlag and Wakeman, 1978; and Ilg, 1979) as well as the present study.

Using the partial correlation coefficients in these regressions, the actual active data were standardized for 10 g fish swimming at 4 $\overline{TL}$ s^{-1} using the following equation:

$$\hat{Y}' = \hat{Y}_A + (1-X_w)\cdot b_w + (4-X_v)\cdot b_v$$

where $\hat{Y}'$ is the standardized rate in log mgO_2hr^{-1}, $\hat{Y}_A$ is the actual rate in log mgO_2hr^{-1}, and the other symbols have their usual meanings. The standardized value ($\hat{Y}'$) was then converted to mgO_2ka^{-1} by taking the antilog and dividing by the standardized weight, 10 g. The regression at 20 ppt for the species and temperature in question was used for standardization of active and resting data. These regressions were also used to calculate the standard metabolic rate of a 10 g fish at the various temperatures and salinities. This procedure involved extrapolation to zero activity and is therefore similar to Brett's (1964) method of estimating the standard rate. It differs in that a multiple regression involving weight as well as velocity was used and all values, rather than just the lowest ones, were considered. The weight used in these calculations is 10 g, hence the standard metabolic rate is also standardized for a 10 g fish. Since the data represented by the multiple regressions in Tables 1 and 2 are for acclimated fish, the estimate of the standard rate is only possible at -1 and 72 hours, if the fish

are assumed acclimated at the end of the experiment rate is constant from the time of the salinity change to the 72-hour value of the standard rate was used for all post change calculations.

Metabolic Scope for Activity

This attribute is defined (Fry, 1947, 1957) as the difference between the active and standard metabolic rates. Biologically, it is a measure of that energy which can be expended aerobically over and above maintenance costs of the organism. Metabolic scope can be used as a convenient measure of sublethal stress (Wohlschlag, 1977). In the present experiment, stress caused by rapid salinity changes is monitored over time so that the timing of the stress and the rate at which it diminishes can be observed.

RESULTS

Preliminary Regression Calculations

The spotted seatrout and red drum regressions relating log oxygen consumption rates to log weights and swimming velocities at 15°C and 28°C are in Tables 1 and 2, respectively. The corresponding statistical data are in Tables 3 and 4, respectively.

Metabolic Responses

The metabolic data for the spotted seatrout and red drum are in Tables 5-10 for the various salinity changes and temperatures. When subjected to rapid salinity changes, the juvenile fishes studied showed metabolic stress responses which began almost immediately. In the majority of cases, stress, as measured by a decrease in metabolic scope, continued to become more severe and reached a critical level (scope minimum) between 6 and 24 hours after the change (see Figures 2-13). Generally, the minimum level is either maintained for several hours or a single critical point is immediately followed by a period of recovery which lasted between 12 and 24 hours after the critical time period. This phase is followed by a period characterized by relative stability.

The pattern described above hold for all except the 20 to 30 ppt change for red drum (Figures 9 and 12). At both 15 and 28°C, this change caused similar responses in the time course. Initially, there was a decrease in scope, and the critical point occurred about one hour after the salinity change.

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Table 1. Multiple regressions relating expected log oxygen consumption rate ($\hat{Y}$) to log body weight (X_w), and velocity ($\overline{TL}$ s^{-1}) at experimental temperatures and salinities. Spotted seatrout.

Equation number	Temp. °C	Equation $\hat{Y} = a + b_w X_w + b_v X_v$	Standardized Standard Rate $mgO_2\ kg^{-1}\ hr^{-1}$
S281	28	$\hat{Y} = -.663 + .990\ X_w + .126\ X_v$	212.1
S282	28	$\hat{Y} = -.542 + .969\ X_w + .124\ X_v$	267.0
S283	28	$\hat{Y} = -.486 + .928\ X_w + .114\ X_v$	277.1
S284	28	$\hat{Y} = -.368 + .875\ X_w + .113\ X_v$	321.5
S151	15	$\hat{Y} = -.879 + 1.005\ X_w + .126\ X_v$	133.6
S152	15	$\hat{Y} = -.860 + .985\ X_w + .172\ X_v$	133.2
S153	15	$\hat{Y} = -.728 + .973\ X_w + .140\ X_v$	176.1
S154	15	$\hat{Y} = -.726 + .982\ X_w + .128\ X_v$	180.3

Table 2. Multiple regressions relating expected log oxygen consumption rate ($\hat{Y}$) to log body weight (X_w), and velocity ($\overline{TL}$ s^{-1}) at experimental temperatures and salinities. Red drum.

Equation number	Temp. ^oC	Equation $\hat{Y} = a + b_w X_w + b_v X_v$	Standardized Standard Rate $mgO_2\ kg^{-1}\ hr^{-1}$
R281	28	$\hat{Y} = -.978 + 1.046\ X_w + .154\ X_v$	117.1
R282	28	$\hat{Y} = -.698 + .935\ X_w + .148\ X_v$	172.5
R283	28	$\hat{Y} = -.667 + .894\ X_w + .162\ X_v$	168.6
R284	28	$\hat{Y} = -.559 + .906\ X_w + .116\ X_v$	222.2
R151	15	$\hat{Y} = -.954 + 1.088\ X_w + .138\ X_v$	136.0
R152	15	$\hat{Y} = -.765 + .948\ X_w + .145\ X_v$	152.5
R153	15	$\hat{Y} = -.715 + .959\ X_w + .135\ X_v$	175.1
R154	15	$\hat{Y} = -.964 + 1.128\ X_w + .153\ X_v$	146.1

Table 3. Multiple regression statistics for equations in Table 1. Spotted seatrout.

Equation number	N	Coefficient of Determination R^2	Standard deviations and Probabilities		
			S_y	S_{b_w}	S_{b_v}
S151	20	0.967	0.0480[a]	0.0073[a]	0.0125[a]
S152	25	0.852	0.1249[a]	0.0179[a]	0.0417[a]
S153	18	0.816	0.2355[a]	0.0069[a]	0.0825[ns]
S154	20	0.962	0.0563[a]	0.0113[a]	0.0164[a]
S281	25	0.937	0.0530[a]	0.0076[a]	0.0080[a]
S282	19	0.992	0.0722[a]	0.0103[a]	0.0169[a]
S283	18	0.971	0.1264[a]	0.0170[a]	0.0196[a]
S284	22	0.982	0.0320[a]	0.0060[a]	0.0061[a]

a-- $p<0.01$

ns-- not significant at 0.05 level

Table 4. Multiple regression statistics for equations in Table 2. Red drum.

Equation number	N	Coefficient of Determination R^2	Standard deviations and Probabilities		
			S_y	S_{b_w}	S_{b_v}
R151	19	0.978	0.0818^a	0.0099^a	0.0190^a
R152	30	0.975	0.0847^a	0.0064^a	0.0177^a
R153	20	0.960	0.2437^a	0.0349^a	0.0741^{ns}
R154	21	0.963	0.1603^a	0.0214^a	0.0435^b
R281	16	0.979	0.0771^a	0.0117^a	0.0197^a
R282	15	0.994	0.1979^a	0.0014^a	0.0150^a
R283	14	0.969	0.1484^a	0.0208^a	0.0279^a
R284	17	0.987	0.0669^a	0.0064^a	0.0093^a

a--$p < 0.01$

b--$0.01 < p < 0.05$

ns--not significant at 0.05 level

Table 5. Time course of resting and 10-g standardized oxygen consumption rates. Spotted seatrout.

Temp. °C	Salinity Change ppt	Time From Change hrs	Average Weight g	N	Resting Rate $mgO_2kg^{-1}hr^{-1}$	Standardized Rate $mgO_2kg^{-1}hr^{-1}$
28	20-10	-1	8.684	19	337.7	336.2
		1	15.1	4	347.0	351.5
		3	15.1	4	276.3	279.9
		6	15.1	4	237.2	240.3
		12	15.1	4	403.6	408.8
		24	15.1	4	247.2	250.4
		30	15.1	4	217.3	220.1
		48	15.1	4	301.5	305.4
		54	15.1	4	199.1	201.7
		72	15.5	3	202.5	205.3
28	20-30	-1	8.684	19	337.7	336.2
		1	5.711	7	373.1	366.7
		3	5.696	7	392.5	385.7
		6	5.300	5	318.0	311.8
		12	6.296	6	402.9	397.1
		24	5.539	7	266.1	261.3
		30	10.773	3	229.7	230.2
		48	10.433	3	282.8	283.2
		54	10.367	3	303.3	306.6
		72	10.03	3	340.7	340.7

Table 5. (cont.)

Temp. °C	Salinity Change ppt	Time From Change hrs	Average Weight g	N	Resting Rate $mgO_2kg^{-1}hr^{-1}$	Standardized Rate $mgO_2kg^{-1}hr^{-1}$
28	20-40	-1	8.684	19	337.7	336.2
		3	8.013	8	314.6	312.4
		6	7.429	7	349.1	345.9
		12	8.013	8	336.2	333.9
		24	7.938	8	383	380.3
		30	7.925	8	339.2	336.8
		48	7.875	8	323.2	320.8
		54	8.371	7	292.6	291.0
15	20-10	-1	15.6	25	139.5	146.5
		1	10.1	8	155.4	155.6
		3	10.1	8	135.1	135.2
		6	10.1	8	209.3	209.5
		12	10.1	7	149.8	150.0
		24	10.0	8	134.6	134.6
		30	9.9	8	168.5	168.3
		48	9.8	8	132.6	132.3
		54	9.7	8	123.0	122.6
		72	10.9	4	96.1	97.0

Table 5. (cont.)

Temp. °C	Salinity Change ppt	Time From Change hrs	Average Weight g	N	Resting Rate $mgO_2kg^{-1}hr^{-1}$	Standardized Rate $mgO_2kg^{-1}hr^{-1}$
15	20-30	-1	15.6	25	139.5	146.5
		1	13.4	11	134.2	138.6
		3	13.2	12	161.3	166.3
		6	13.2	12	135.6	139.8
		12	13.2	12	143.8	148.3
		24	13.2	12	109.3	112.7
		30	13.2	12	126.1	130.0
		48	13.1	11	110.0	113.3
		54	13.1	12	149.7	154.2
		72	13.1	12	122.1	125.8
15	20-40	-1	15.6	25	139.5	146.5
		3	27.6	6	115.0	128.6
		6	27.6	6	155.7	174.1
		12	30.2	5	173.2	195.5
		24	18.5	4	114.8	122.8
		30	18.4	4	98.0	104.7
		48	18.1	4	119.1	127.1
		54	18.0	4	112.2	119.7
		72	17.7	4	133.0	141.6

Table 6. Time course of resting and 10-g standardized oxygen consumption rates. Red drum.

Temp. °C	Salinity Change ppt	Time From Change hrs	Average Weight g	N	Resting Rate $mgO_2kg^{-1}hr^{-1}$	Standardized Rate $mgO_2kg^{-1}hr^{-1}$
28	20-10	-1	15.36	18	381.0	383.5
		1	2.113	4	520.1	507.9
		3	2.113	4	437.7	427.5
		6	2.275	2	543.7	531.6
		12	2.038	4	473.9	462.6
		24	1.963	4	568.3	554.4
		30	1.867	3	479.7	467.6
		48	1.800	4	491.1	478.4
		54	1.775	4	506.2	493.1
		72	1.650	4	589.0	573.1
28	20-30	-1	15.36	18	381.0	383.5
		1	14.044	8	447.0	449.3
		3	14.019	8	411.4	413.5
		6	9.579	7	366.5	366.3
		12	15.657	7	339.2	341.5
		24	13.781	8	384.0	385.9
		30	13.700	8	333.7	335.3
		48	13.525	8	429.8	431.8
		54	13.293	7	437.5	439.4
		72	14.903	7	386.4	388.8

Table 6. (cont.)

Temp. °C	Salinity Change ppt	Time From Change hrs	Average Weight g	N	Resting Rate $mgO_2kg^{-1}hr^{-1}$	Standardized Rate $mgO_2kg^{-1}hr^{-1}$
28	20-40	-1	15.360	18	381.0	383.5
		3	22.443	7	352.9	357.3
		6	22.429	7	373.2	377.8
		12	30.73	5	268.1	272.7
		24	25.846	6	325.6	330.3
15	20-10	-1	3.36	34	214.0	206.3
		1	3.83	12	182.0	176.2
		3	3.65	11	229.2	221.5
		6	3.82	12	153.1	148.2
		12	3.84	11	234.7	227.3
		24	3.76	12	191.2	185.0
		30	3.79	11	205.8	199.2
		48	3.71	12	203.4	196.7
		54	3.68	12	167.9	162.3
		72	3.61	11	184.3	178.1
15	20-30	-1	3.360	34	214.0	206.3
		1	1.540	11	246.0	231.0
		3	2.405	10	224.6	214.1
		6	2.825	8	245.7	235.5
		12	2.450	11	213.3	203.4
		24	2.720	9	186.3	178.3
		30	2.940	8	169.1	162.3

Table 6. (cont.)

Temp. °C	Salinity Change ppt	Time From Change hrs	Average Weight g	N	Resting Rate $mgO_2kg^{-1}hr^{-1}$	Standardized Rate $mgO_2kg^{-1}hr^{-1}$
		48	2.305	11	249.4	237.4
		54	2.220	12	203.9	193.8
		72	2.580	9	197.7	188.9
15	20-40	-1	3.36	34	214.0	206.3
		3	3.75	12	187.0	180.9
		6	3.79	12	184.1	178.2
		12	3.78	11	190.4	184.3
		24	3.65	12	255.8	247.3
		30	3.66	12	158.5	153.2
		48	3.48	11	190.9	184.2
		54	3.72	10	170.3	164.7
		72	3.45	12	193.3	186.5

Table 7. Time course of active and 10-g, 4 TL/S standardized oxygen consumption rates. Spotted seatrout.

Temp. °C.	Salinity Change ppt	Time from Change hrs	No. of Fish	Average Total Length cm	Average Weight g	Velocity TL/S	Active Rate $mgO_2kg^{-1}hr^{-1}$	10g-4 TL/S Standardized Rate $mgO_2kg^{-1}hr^{-1}$
28	20-10	-1	3	21.17	73.77	3.670	889.9	1088.8
			1	22.8	106.0	4.009	780.8	936.6
		1	3	21.17	73.77	3.670	650.3	795.7
			1	22.8	106.0	4.009	814.7	977.1
		3	3	21.17	73.77	3.670	700.4	856.9
			1	22.8	106.0	4.009	678.9	814.2
		6	3	21.17	73.77	3.670	574.7	703.1
			1	22.8	106.0	4.009	733.9	880.3
		12	3	21.17	73.77	3.238	537.3	699.5
			1	22.8	105.0	4.009	599.7	718.5
		24	2	20.60	66.65	3.771	503.8	602.7
			1	22.8	104.0	4.009	641.3	767.6

	30	2	20.6	66.65	3.771	785.2	839.8
		1	22.8	104.0	4.009	618.3	740.2
	48	2	20.6	66.65	3.771	664.4	794.7
		1	22.8	102	4.009	651.2	777.5
	54	2	20.6	66.65	3.771	647.8	775.0
		1	22.8	101.0	4.009	746.4	891.9
	72	2	20.6	66.65	3.771	647.8	775.0
		1	22.8	100.0	4.009	811.8	968.7
20-30	-1	5	11.3	11.9	3.438	945.6	1038.2
		7	12.6	15.5	5.078	817.2	723.5
	1	5	11.3	11.9	3.438	969.4	1064.3
		7	12.6	15.5	5.078	661.4	585.5
	3	5	11.3	11.9	3.438	908.3	996.5
		7	12.6	15.5	5.078	757.1	670.3
	6	5	11.3	11.9	3.438	772.4	846.8
		7	12.6	15.5	5.078	648.1	573.8
	12	5	11.3	11.8	3.438	642.9	708.4
		7	12.6	15.5	5.078	911.6	807.0

	24	5	11.3	11.8	3.438	676.4	687.8
		4	13.2	16.8	4.847	1064.0	979.1
	30	5	11.3	11.8	3.438	975.3	1067.5
		4	14.4	21.65	5.078	979.6	891.0
	48	5	11.3	11.7	3.438	1199.8	1315.4
		4	14.4	21.65	5.078	778.2	707.7
	54	5	11.3	11.7	3.438	1154.2	1263.1
		4	14.4	21.65	5.078	959.9	873.1
	72	5	11.3	11.6	3.438	1172.8	1285.4
		4	14.4	21.65	5.078	920.7	837.5
20-40	-1	7	9.61	7.83	3.804	843.6	850.9
		7	10.33	8.61	3.318	939.3	1026.1
	3	7	9.61	7.77	3.567	613.4	641.1
		7	10.33	8.61	3.318	961.3	1049.1
	6	7	9.61	7.70	3.804	587.4	592.7
		7	10.33	8.61	3.318	862.6	941.2
	12	7	9.61	7.59	3.804	761.9	767.2
		7	10.33	8.61	3.539	1118.2	1181.8
	24	7	9.61	7.33	3.804	715.3	718.4
		7	10.33	8.61	3.539	780.4	825.0

30	7	9.61	7.21	3.804	775.3	777.9
	7	10.33	8.61	3.539	1006.4	1063.8
48	7	9.61	6.84	3.804	797.7	854.5
	7	10.33	8.61	3.539	862.6	911.7
54	7	9.61	6.71	3.804	659.3	657.7
	7	10.33	8.61	3.539	834.6	822.2
72	7	9.61	6.33	-	-	-
	7	10.33	8.61	3.539	842.6	890.5

Table 8. Time course of active and 10-g, 4 TL/S standardized oxygen consumption rates. Spotted seatrout.

Temp. °C.	Salinity Change ppt	Time from Change hrs	No. of Fish	Average Total Length cm	Average Weight g	Velocity TL/S	Active Rate $mgO_2kg^{-1}hr^{-1}$	10g-4 TL/S Standardized Rate $mgO_2kg^{-1}hr^{-1}$
15	20-10	-1	4	13.25	17.6	3.713	545.4	616.4
			7	10.16	8.44	3.834	697.4	743.0
			6	13.05	17.7	3.456	618.5	774.3
		1	4	13.25	17.6	4.177	550.8	518.2
			7	10.16	8.43	3.632	442.7	510.5
			6	13.05	17.7	3.456	350.5	438.4
		3	4	13.25	17.6	9.177	459.8	432.7
			7	10.16	8.43	3.632	464.9	536.0
			6	13.05	17.7	3.456	370.2	463.1
		6	4	13.25	17.6	4.177	539.5	507.5
			7	10.16	8.40	3.834	311.3	331.6
			6	13.05	17.7	3.456	385.5	482.1

	12	4	13.25	17.6	4.177	513.0	482.1
		7	10.16	8.37	3.834	459.2	489.1
		6	13.05	17.7	3.456	382.4	478.5
	24	4	13.25	17.6	4.177	514.8	483.4
		7	10.16	8.31	3.834	602.5	642.7
		6	13.05	17.7	3.456	362.6	453.7
	30	4	13.25	17.6	3.249	252.1	341.6
		7	10.16	8.28	3.834	468.0	498.0
		6	13.05	17.7	3.456	415.1	519.5
	48	4	13.25	17.6	4.177	529.5	496.9
		7	10.16	8.18	3.834	464.0	494.6
		6	13.05	17.7	3.456	346.4	446.2
	54	4	13.25	17.6	4.177	575.5	540.9
		7	10.16	8.16	3.834	486.5	518.2
		6	13.05	17.7	3.456	408.1	510.3
	72	4	13.25	17.6	4.332	568.1	499.8
		7	10.16	8.06	3.834	492.5	524.5
		6	13.05	17.7	3.456	-	-
20-30	-1	6	10.2	7.8	3.6176	723.4	842.3
		6	11.9	12.6	4.1344	565.1	536.2

	1	6	10.2	7.8	3.6176	537.65	624.7
		6	11.9	17.6	4.1344	600.151	569.5
	3	6	10.2	7.8	3.6176	615.3	714.9
		6	11.9	12.6	4.3067	527.7	467.6
	6	6	10.2	7.8	3.6176	362.8	420.7
		6	11.9	12.6	4.3067	596.3	528.3
	12	6	10.2	7.8	3.6176	364.4	420.7
		6	11.9	12.6	4.3067	437.2	387.4
	24	6	10.2	7.7	3.6176	441.4	511.6
		6	11.9	12.6	4.3067	326.7	289.4
	30	6	10.2	7.7	3.6176	410.2	242.9
		6	11.9	12.6	4.1344	400.81	380.2
	48	5	10.2	9.1	3.6176	595.5	700.0
		6	12.0	13.2	4.2708	516.7	388.4
	54	5	10.2	9.1	3.6176	501.9	580.8
		6	12.0	13.2	4.1000	543.0	436.7
	72	5	10.2	9.0	3.8186	545.1	581.8
		6	12.0	13.2	4.2708	582.8	438.0
20-40	-1	6	10.3	9.00	3.1844	572.4	789.8
		3	19.4	49.80	2.642	270.6	475.2
	3	6	10.3	8.93	3.1844	492.1	679.0
		3	19.4	49.8	2.642	191.7	336.7

6	6	10.3	8.87	3.1844	361.0	497.9
	3	19.4	49.8	2.642	303.9	533.7
12	6	10.3	8.75	3.1844	385.4	531.7
	3	19.4	49.8	2.642	239.6	420.9
24	5	10.0	8.28	3.28	463.0	614.3
	3	19.4	49.8	2.642	285.4	79.3
30	4	10.0	8.80	3.28	406.6	723.1
	3	19.4	49.8	2.642	307.7	540.5
48	4	10.0	8.225	3.28	508.4	674.5
	2	19.1	52.1	2.683	317.6	549.2
54	4	10.1	8.05	3.25	503.15	675.3
	2	19.1	52.1	2.683	323.7	559.8
72	3	10.4	8.27	3.15	-	-
	2	19.1	52.1	2.683	357.3	617.8

Table 9. Time course of active and 10-g, 4 TL/S standardized oxygen consumption rates. Red drum.

Temp. °C.	Salinity Change ppt	Time from Change hrs	No. of Fish	Average Total Length cm	Average Weight g	Velocity TL/S	Active Rate $mgO_2kg^{-1}hr^{-1}$	10g-4 TL/S Standardized $mgO_2kg^{-1}hr^{-1}$
28	20-10	-1	33	6.12	1.985	6.347	1477.8	597.7
			1	24.8	147.5	3.685	594.7	788.8
		1	33	6.12	1.9788	6.347	1322.4	637.8
			1	24.8	147.3	2.685	558.3	740.8
		3	33	6.12	1.9667	6.347	887.0	561.4
			1	24.8	147.0	3.685	575.9	386.7
		6	33	6.12	1.9515	6.347	854.5	482.7
			1	24.8	146.5	3.685	466.2	192
		12	33	6.12	1.9182	6.347	909.5	444.2
			1	24.8	145.4	3.685	395.9	109.1
		24	33	6.12	1.8545	6.347	1014.5	550.1
			1	24.8	143.3	3.685	522.3	691.7
		30	33	6.12	1.8212	6.347	1004.2	455.6
			1	24.8	142.3	3.870	408.1	507.3

	48	33	6.12	1.7212	6.347	1351.4	541.5
		1	24.8	139.2	3.685	480.9	635.8
	54	33	6.12	1.6879	6.347	1033.	413.7
		1	24.8	138.1	3.685	467.2	617.3
	72	33	6.12	1.5848	6.347	1017.	405.3
		1	24.8	135.0	3.685	355.4	468.9
20-30	-1	1	18.7	67.5	3.421	636.1	877.8
		37	6.235	1.81	4.764	1125.8	774.2
	1	1	18.7	67.4	3.421	580.1	799.9
		37	6.235	1.81	4.764	815.9	562.6
	3	1	18.7	67.3	3.421	565.6	780.2
		37	6.235	1.805	4.764	1240.7	855.2
	6	1	18.7	67.1	3.421	744.5	1026.8
		37	6.235	1.797	4.764	1150.8	793.1
	12	1	18.7	66.8	3.421	641.0	833.9
		37	6.235	1.7811	5.131	1352.6	822.2
	24	1	18.7	66.2	3.421	659.8	909.1
		37	6.235	1.7486	5.131	916.4	556.3
	30	1	18.7	65.9	3.421	722.0	994.5
		37	6.235	1.73	5.131	1002.1	607.8

48	1	18.7	65.0	3.421	614.9	846.3
	37	6.235	1.68	5.131	1489.2	901.9
54	1	18.7	64.7	3.421	774.8	1066.1
	37	6.235	1.67	4.764	1330.2	912.2
72	1	18.7	63.8	3.421	698.6	1129.7
	37	6.235	1.62	4.764	1072.3	734.1
-1	2	17.6	65.5	5.193	822.5	619.3
	31	6.03	1.82	6.063	1444.0	640.7
3	2	17.6	65.5	5.193	641.4	482.4
	31	6.03	1.79	6.063	896.2	396.6
6	2	17.6	65.5	5.193	641.4	482.9
	31	6.03	1.76	6.063	-	-
12	2	17.6	65.5	5.193	533.4	401.6
	29	6.03	1.70	6.063	1273.4	561.6
24	2	17.6	65.5	5.193	579.1	436.0
	20	6.03	1.59	6.063	1201.5	527.6
30	2	17.6	65.5		Dead	-
	18	6.03	1.35	6.063	1418.6	697.6
48					Dead	
					Dead	

Table 10. Time course of active and 10-g, 4 TL/S standardized oxygen consumption rates. Red drum.

Temp. °C.	Salinity Change ppt	Time from Change hrs	No. of Fish	Average Total Length cm	Average Weight g	Velocity TL/S	Active Rate $mgO_2kg^{-1}hr^{-1}$	10g-4 TL/S Standardized Rate $mgO_2kg^{-1}hr^{-1}$
15	20-10	-1	17	6.48	2.56	4.745	1150.5	835.8
			19	6.48	2.44	4.429	709.3	571.5
			7	9.39	9.171	4.585	610.3	499.8
		1	17	6.48	2.56	4.745	843.6	612.9
			19	6.48	2.43	4.429	340.4	274.2
			7	9.39	9.1	4.366	568.1	500.3
		3	17	6.48	2.56	5.062	713.1	466.0
			19	6.48	2.43	4.429	692.1	557.5
			7	9.39	9.04	4.366	452.3	398.2
		6	17	6.48	2.56	5.062	394.9	258.1
			19	6.48	2.42	5.694	599.4	316.3
			7	9.39	8.94	4.366	517.1	454.9

12	17	6.48	2.56	5.062	561.1	366.7
	19	6.48	2.40	5.062	518.3	337.7
	7	9.39	8.76	4.366	552.0	485.1
24	17	6.48	2.56	4.745	723.1	525.4
	19	6.48	2.36	5.062	843.1	548.9
	7	9.59	8.37	4.366	479.4	420.3
30	17	6.48	2.56	5.062	633.8	414.2
	19	6.48	2.34	4.745	567.1	410.3
	7	9.39	8.21	4.366	565.5	495.0
48	17	6.48	2.56	5.062	611.2	399.4
	19	6.48	2.28	5.062	670.1	435.4
	7	9.39	7.60	4.366	-	-
54	17	6.48	2.56	5.062	420.8	275.0
	19	6.48	2.27	5.062	533.1	345.6
	7	9.39	7.41	4.366	551.7	480.7
72	17	6.48	2.56	5.062	668.5	426.8
	19	6.48	2.21	5.062	651.7	422.8
	7	9.59	6.84	4.366	555.1	481.7

20-30	-1	15	5.43	1.46	4.91	1326.9	890.6
		17	5.18	1.13	4.83	-	
		18	5.79	1.82	4.18	628.3	511.9
	1	15	5.43	1.46	4.91	749.3	502.9
		17	5.18	1.13	4.60	572.4	418.3
		18	5.79	1.87	3.89	335.6	318.9
	3	15	5.43	1.46	4.91	856.3	574.7
		17	5.18	1.13	5.14	858.6	523.9
		18	5.79	1.811	4.04	954.1	862.1
	6	15	5.43	1.45	4.91	1498.6	1005.7
		17	5.18	1.12	5.14	1438.4	880.8
		18	5.79	1.81	3.89	1183.1	1124.0
	12	14	5.45	1.52	4.89	1031.9	690.4
		17	5.18	1.12	5.14	1414.8	866.3
		18	5.79	1.79	3.89	664.4	630.8
	24	14	5.45	1.52	4.89	814.6	549.6
		17	5.18	1.11	5.14	1453.7	888.3
		18	5.79	1.76	3.89	683.5	648.4
	30	14	5.45	1.52	-	-	-
		17	5.18	1.11	5.14	844.1	515.8
		18	5.79	1.74	3.89	876.6	831.1

	48	12	5.54	1.66	4.81	1123.2	780.3
		17	5.18	1.10	5.14	1156.1	704.9
		18	5.79	1.69	3.89	1123.21	1063.2
	54	12	5.66	1.62	-	-	-
		17	5.18	1.09	5.14	1661.7	1016.6
		18	5.79	1.68	3.89	1057.3	1000.5
	72	12	5.66	1.62	4.71	1019.7	730.8
		15	5.18	1.0	5.14	-	-
		18	5.79	1.63	3.89	527.4	498.4
20-40	-1	25	6.22	2.07	4.944	677.6	455.6
		9	8.48	4.94	4.351	726.7	623.2
		25	6.39	2.20	4.170	706.4	617.4
	3	25	6.22	2.06	4.614	367.1	275.6
		9	8.48	4.93	4.110	480.4	446.6
		24	6.39	3.30	4.170	579.8	506.6
	6	25	6.22	2.05	4.614	415.8	312.2
		9	8.48	4.93	4.351	427.8	366.9
		24	6.39	2.19	4.170	492.5	430.3
	12	24	6.22	2.03	4.944	413.8	277.3
		9	8.48	4.91	3.868	382.9	385.8
		24	6.39	2.158	4.170	449.2	392.2

24	23	6.23	1.99	4.936	692.9	466.4
	9	8.48	4.89	3.868	556.7	560.8
	24	6.39	2.1125	4.170	420.0	366.2
30	23	6.23	1.97	4.936	591.9	398.1
	9	8.48	4.88	3.868	527.5	67.0
	24	6.39	2.09	4.170	549.4	478.8
48	23	6.23	1.91	4.936	627.0	421.1
	9	8.48	4.83	4.110	537.4	499.0
	23	6.39	2.02	4.170	444.8	387.0
54	23	6.23	1.89	4.936	594.4	398.9
	9	8.48	4.82	4.110	595.8	553.1
	23	6.39	2.00	4.170	572.9	498.0
72	23	6.23	1.83	4.936	579.7	388.4
	9	8.48	4.78	4.351	601.3	514.8
	23	6.39	1.92	4.170	596.0	517.3

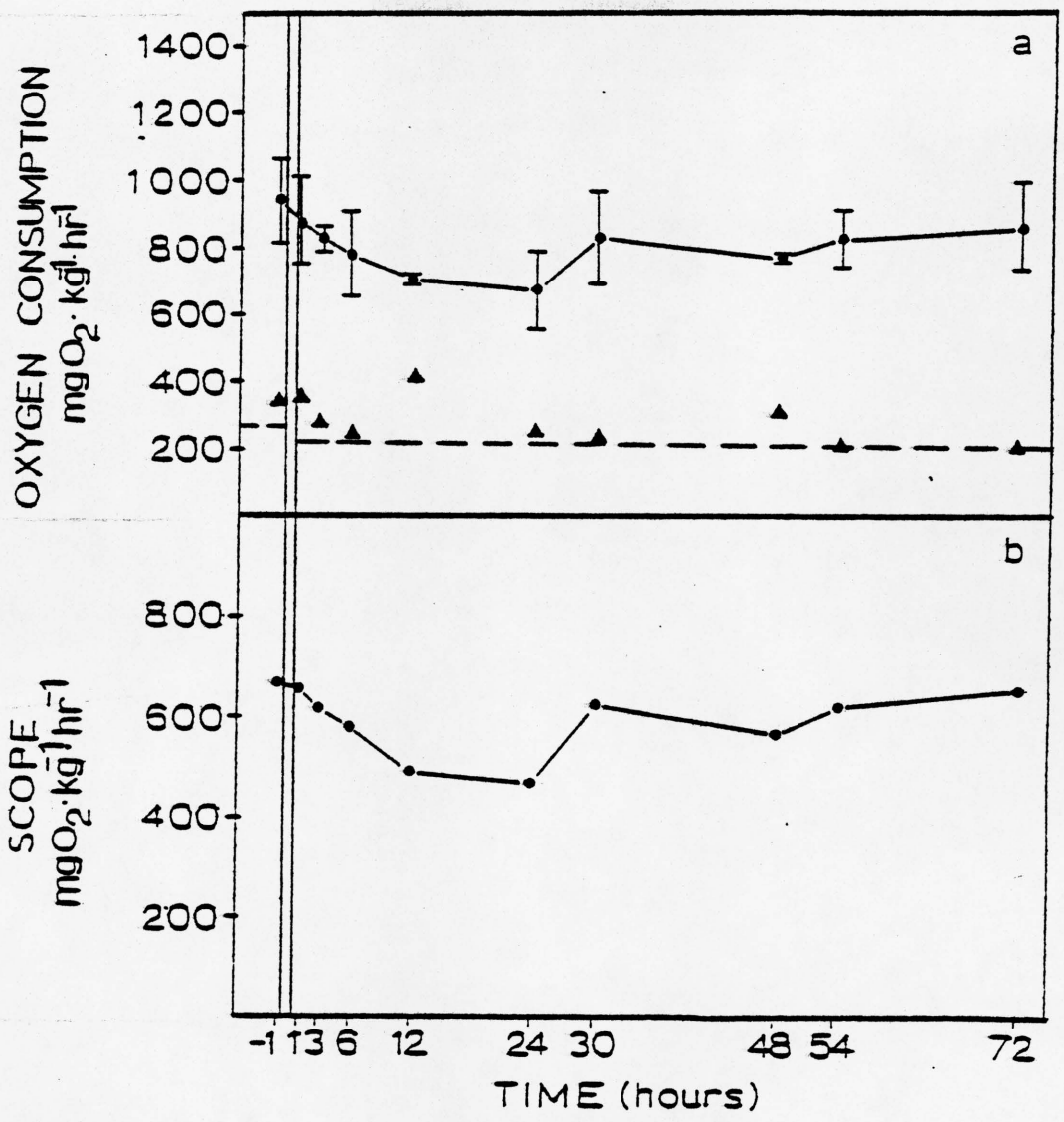


Figure 2. Spotted seatrout 28°C, 20-10 ppt.--(a) Time course of ● active (4 TL/s), and ▲ resting (0 TL/s) oxygen consumption following a one hour salinity change from 20 to 10 ppt standardized for a 10 g fish. Dashed line is calculated standard metabolic rate. (b) Time course of ● metabolic scope for activity.

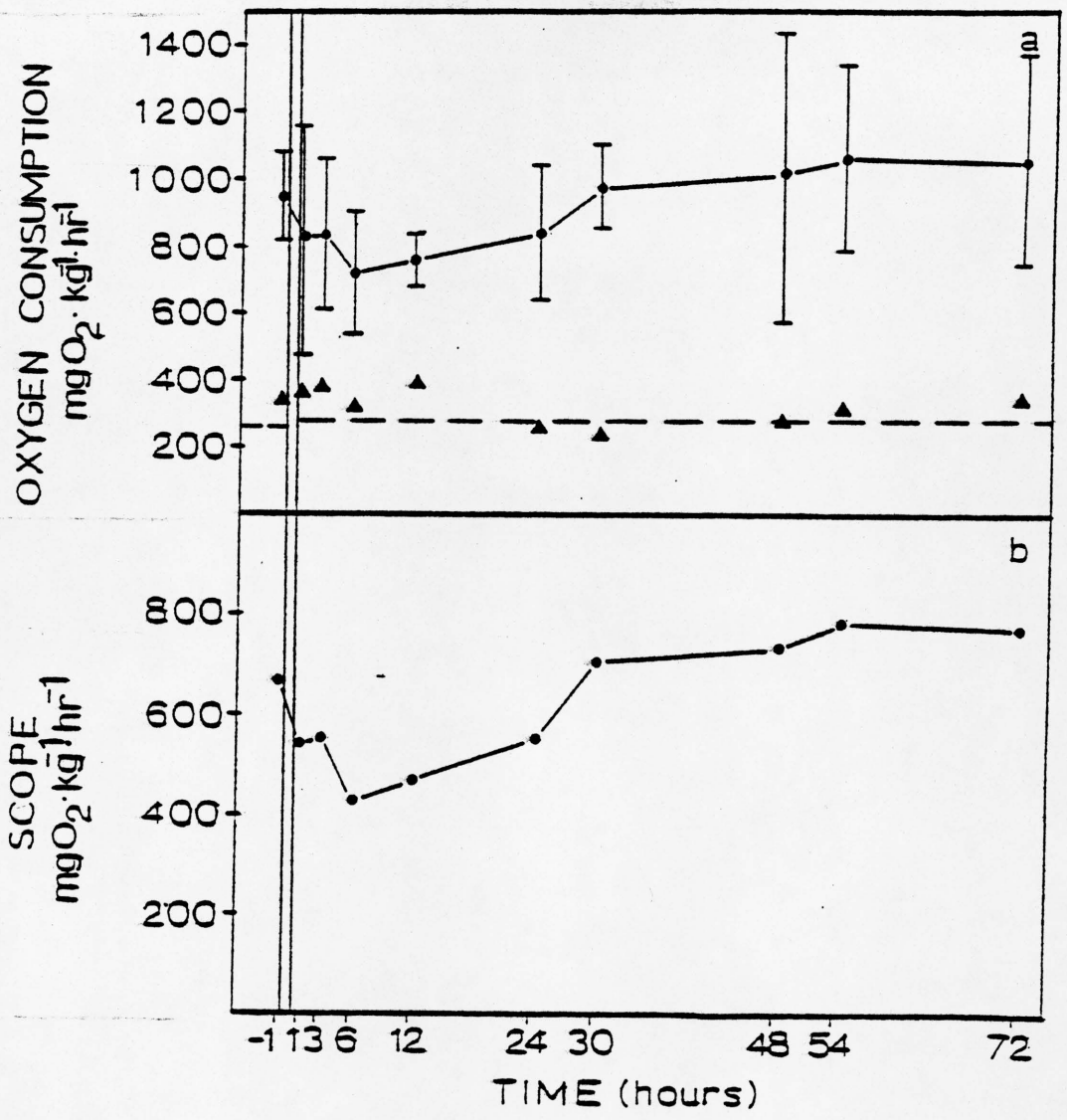


Figure 3. Spotted seatrout 28°C, 20-30 ppt.--(a) Time course of ● active (4 TL/s), and ▲ resting (0 TL/s) oxygen consumption following a one hour salinity change from 20 to 30 ppt standardized for a 10 g fish. Dashed line is calculated standard metabolic rate. (b) Time course of ● metabolic scope for activity.

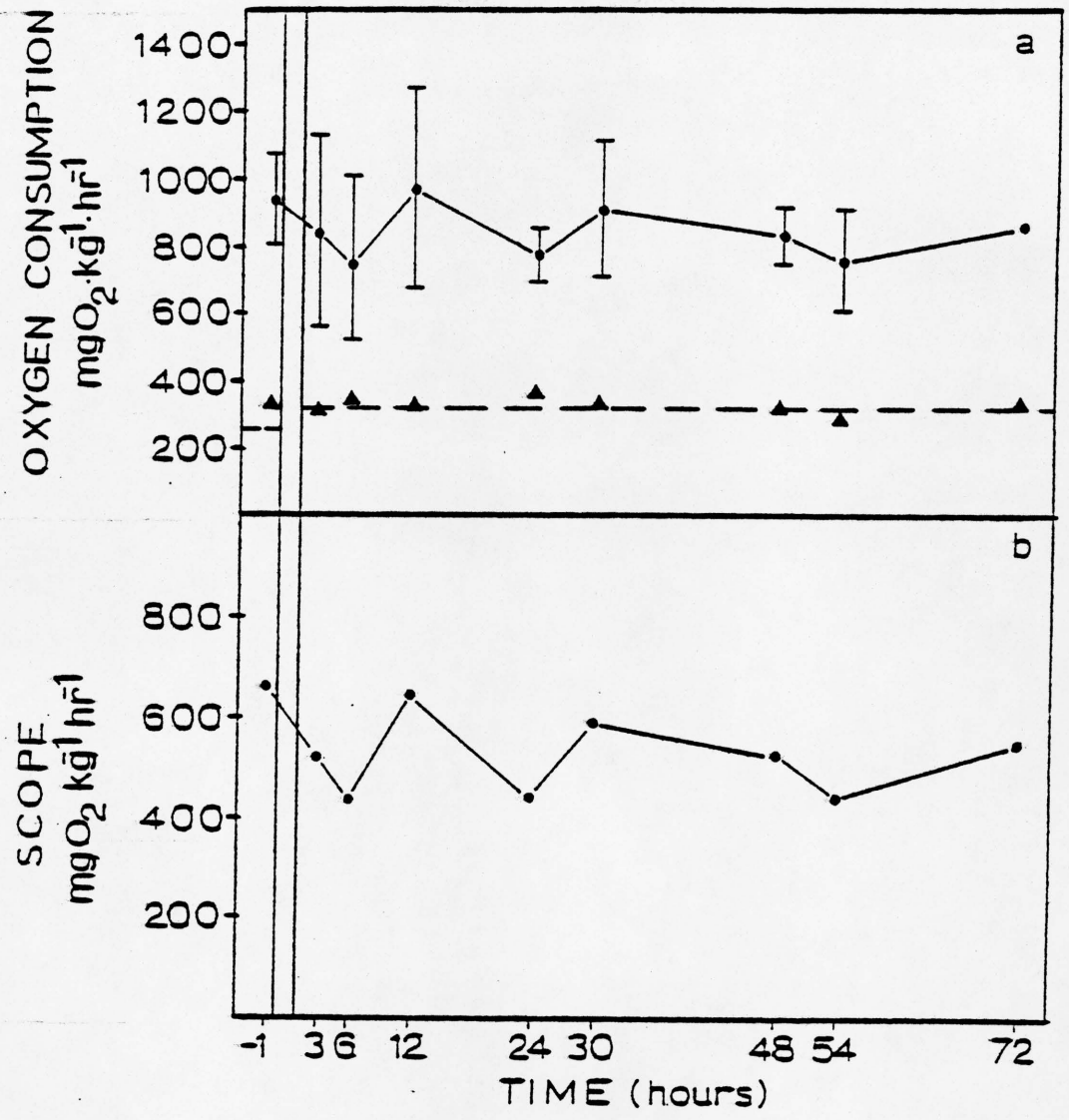


Figure 4. Spotted seatrout 28°C, 20-40 ppt.--(a) Time course of ● active (4 TL/s), and ▲ resting (0 TL/s) oxygen consumption following a two hour salinity change from 20 to 40 ppt standardized for a 10 g fish. Dashed line is calculated standard metabolic rate. (b) Time course of ● metabolic scope for activity.

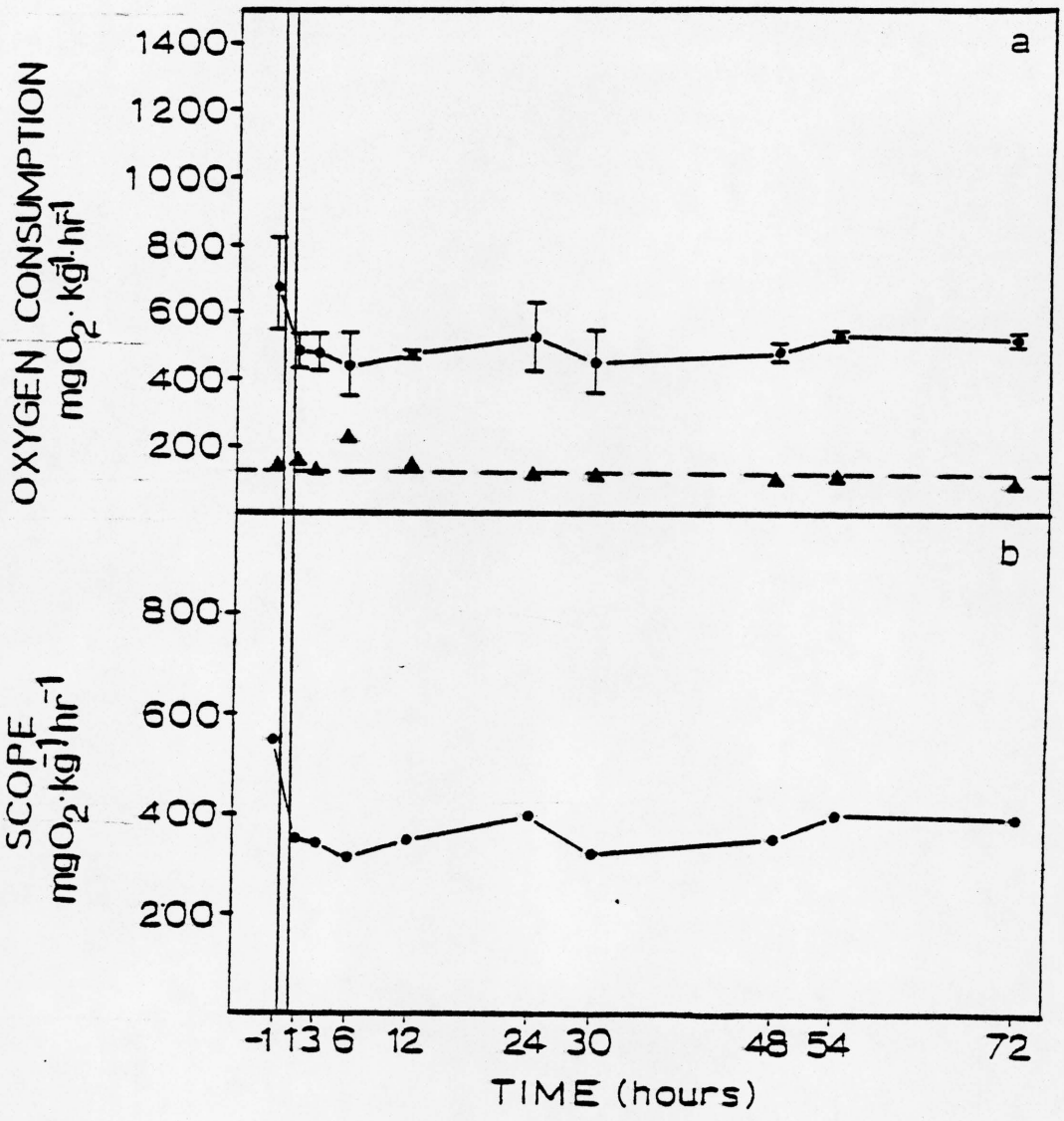


Figure 5. Spotted seatrout 15°C, 20-10 ppt.--(a) Time course of ● active (4 TL/s), and ▲ resting (0 TL/s) oxygen consumption following a one hour salinity change from 20 to 10 ppt standardized for a 10 g fish. Dashed line is calculated standard metabolic rate. (b) Time course of ● metabolic scope for activity.

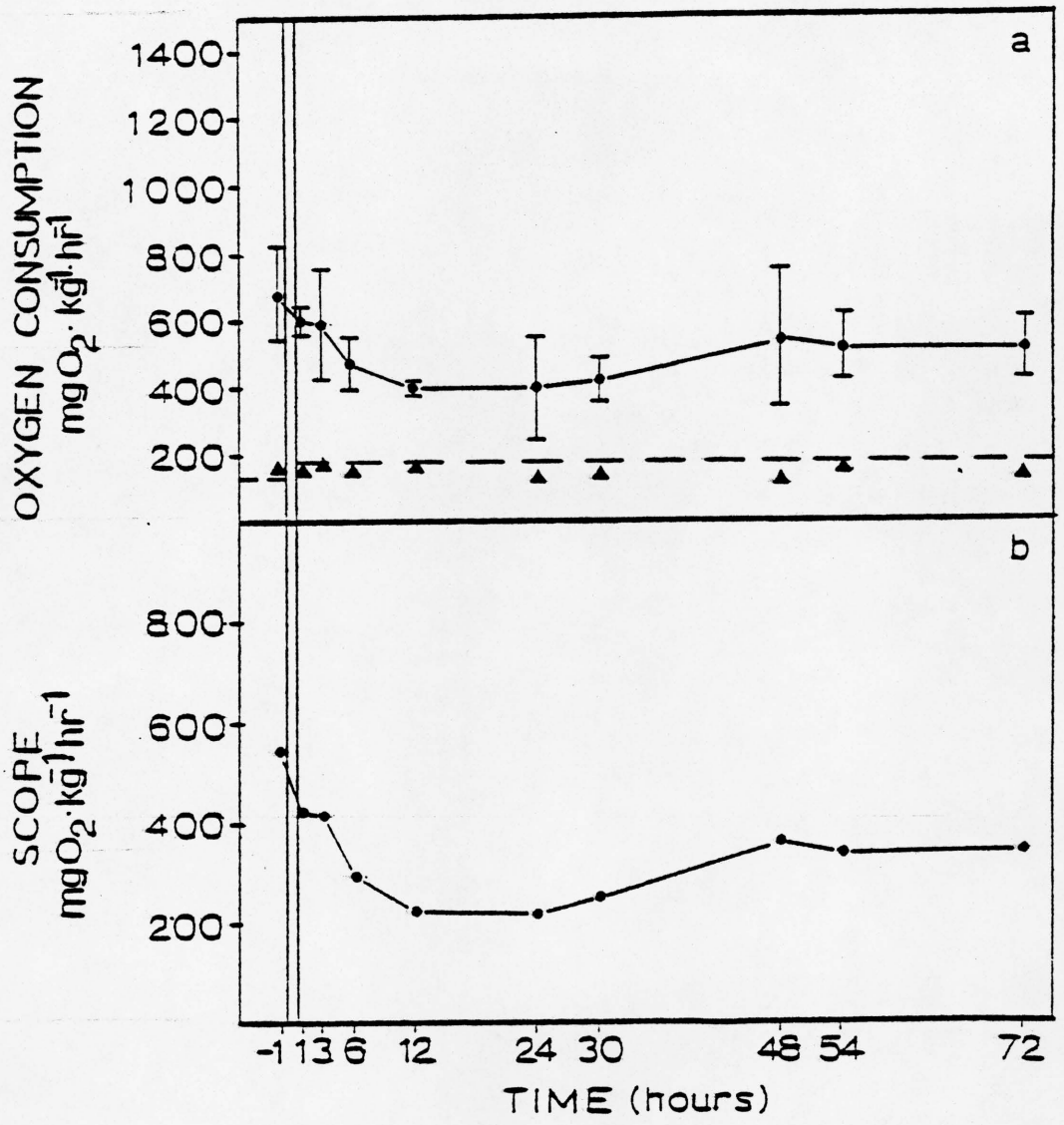


Figure 6. Spotted seatrout 15°C, 20-30 ppt.--(a) Time course of ● active (4 TL/s), and ▲ resting (0 TL/s) oxygen consumption following a one hour salinity change from 20 to 30 ppt standardized for a 10 g fish. Dashed line is calculated standard metabolic rate. (b) Time course of metabolic scope for activity.

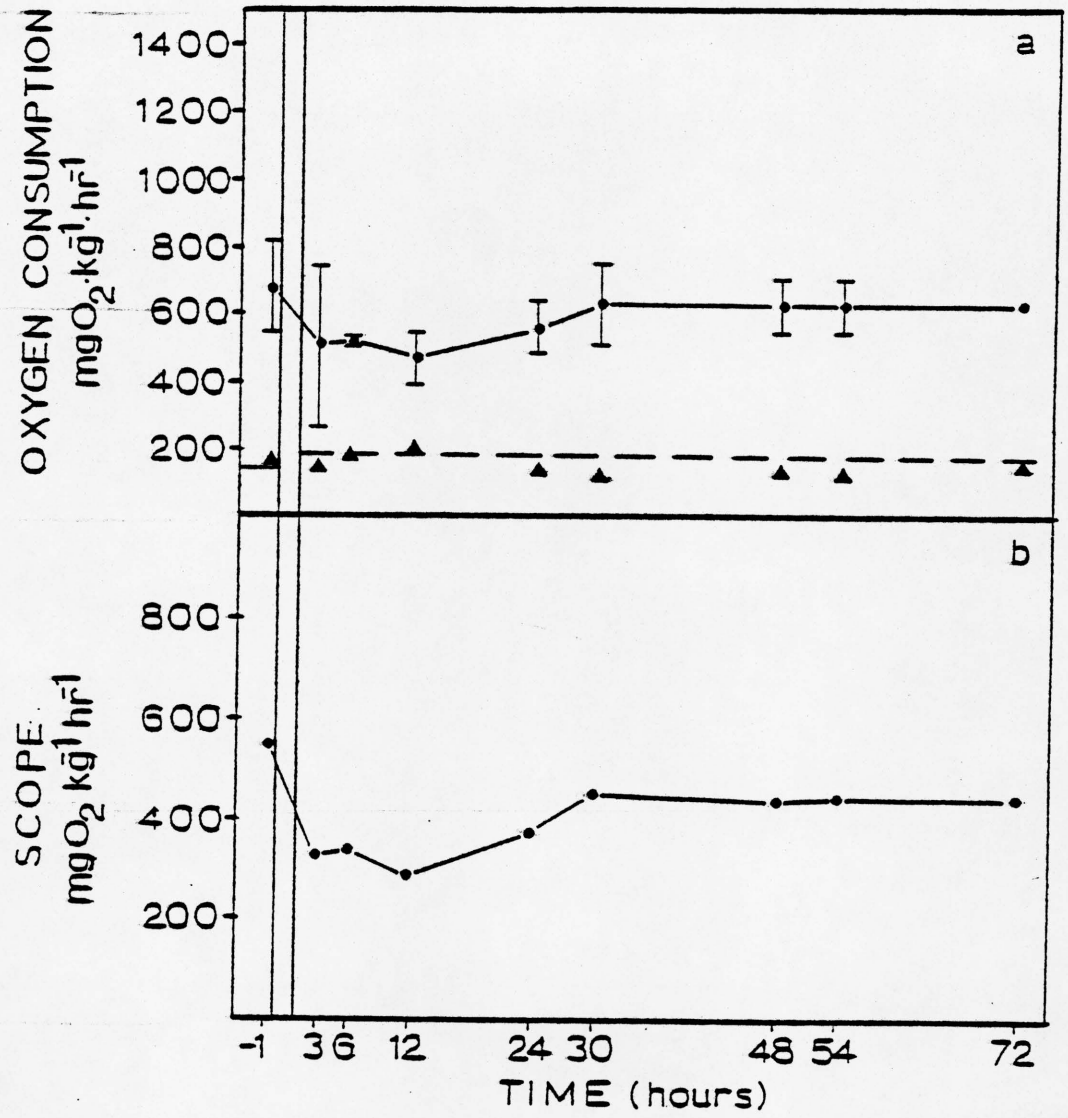


Figure 7. Spotted seatrout 15°C, 20-40 ppt.--(a) Time course of ● active (4 TL/s), and ▲ resting (0 TL/s) oxygen consumption following a two hour salinity change from 20 to 40 ppt standardized for a 10 g fish. Dashed line is calculated standard metabolic rate. (b) Time course of ● metabolic scope for activity.

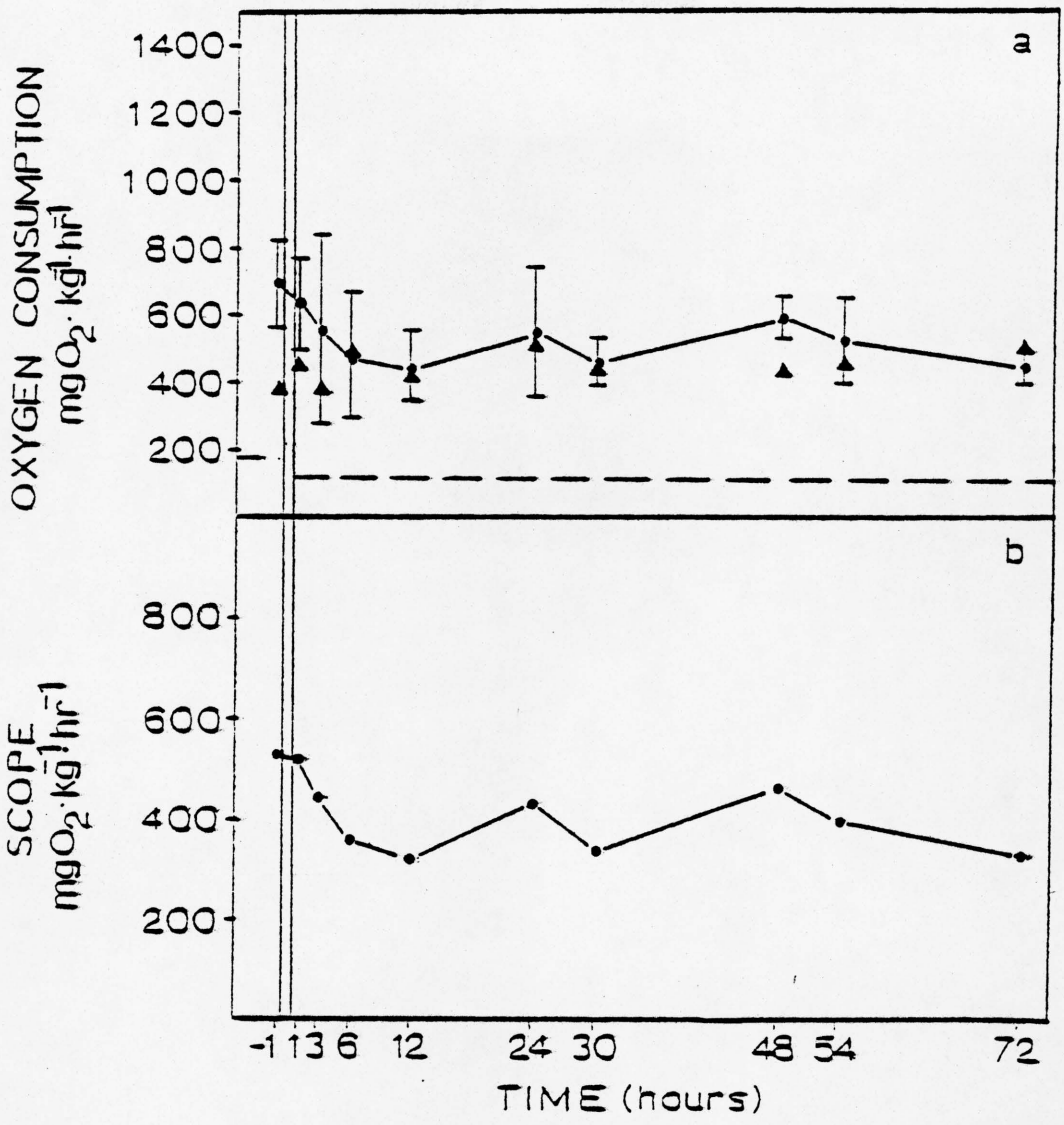


Figure 8. Red drum 28°C, 20-10 ppt.--(a) Time course of ● active (4 TL/s), and ▲ resting (0 TL/s) oxygen consumption following a one hour salinity change from 20 to 10 ppt standardized for a 10 g fish. Dashed line is calculated standard metabolic rate. (b) Time course of ● metabolic scope for activity.

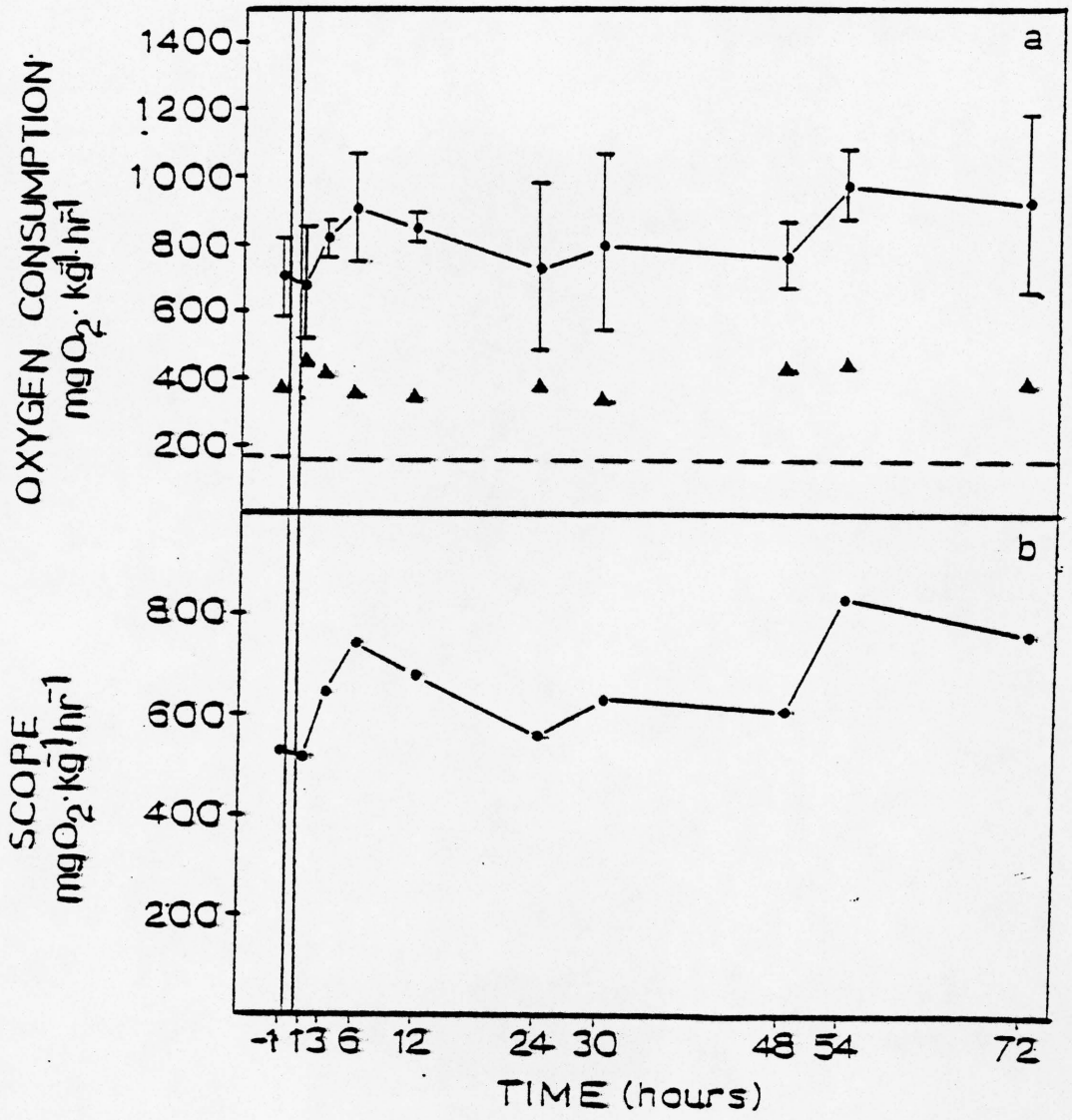


Figure 9. Red drum 28°C, 20-30 ppt.--(a) Time course of ● active (4 TL/s), and ▲ resting (0 TL/s) oxygen consumption following a one hour salinity change from 20 to 30 ppt standardized for a 10 g fish. Dashed line is calculated standard metabolic rate. (b) Time course of ● metabolic scope for activity.

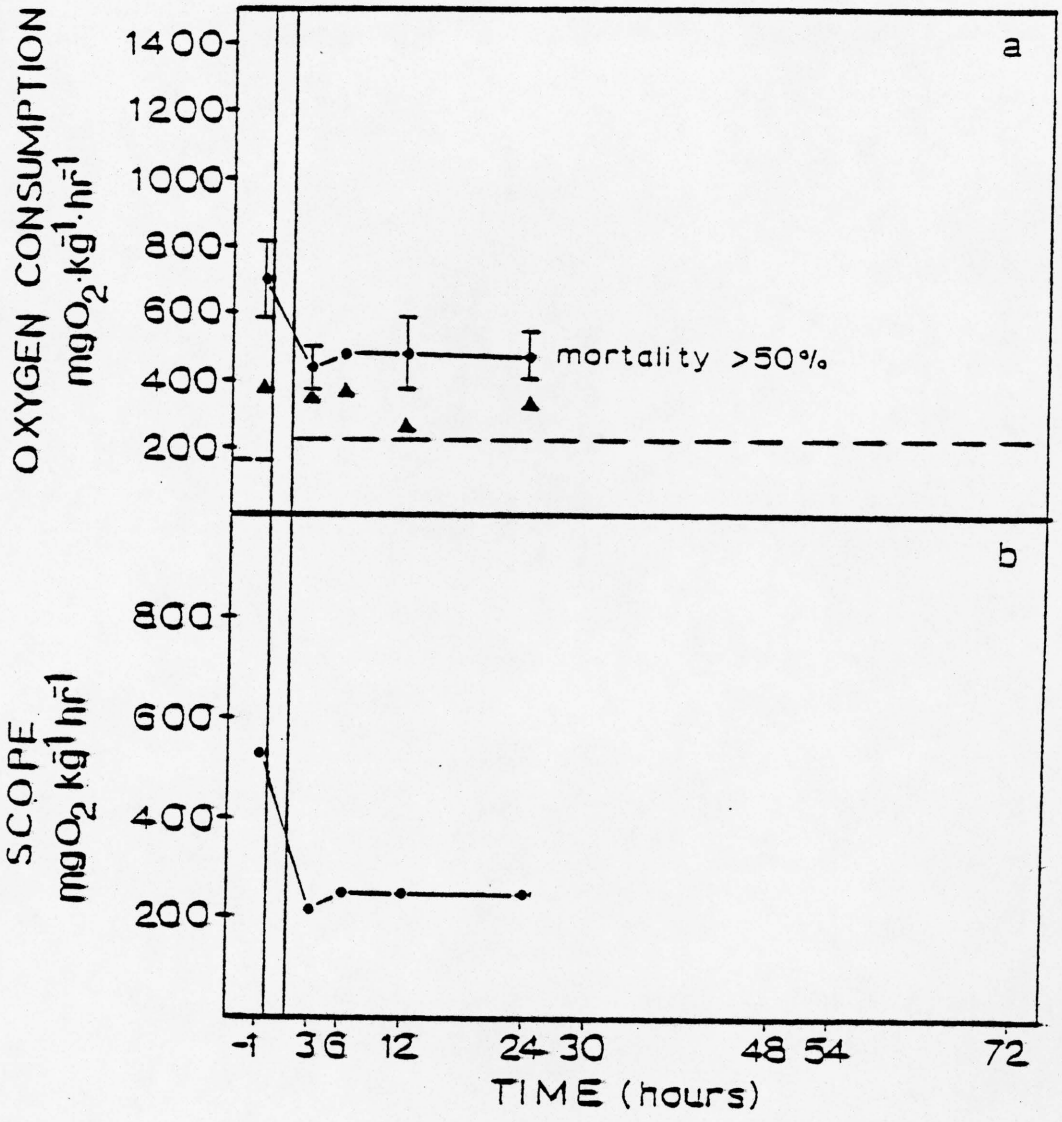


Figure 10. Red drum 28°C, 20-40 ppt.--(a) Time course of ● active (4 TL/s), and ▲ resting (0 TL/s) oxygen consumption following a two hour salinity change from 20 to 40 ppt standardized for a 10 g fish. Dashed line is calculated standard metabolic rate. (b) Time course of ● metabolic scope for activity.

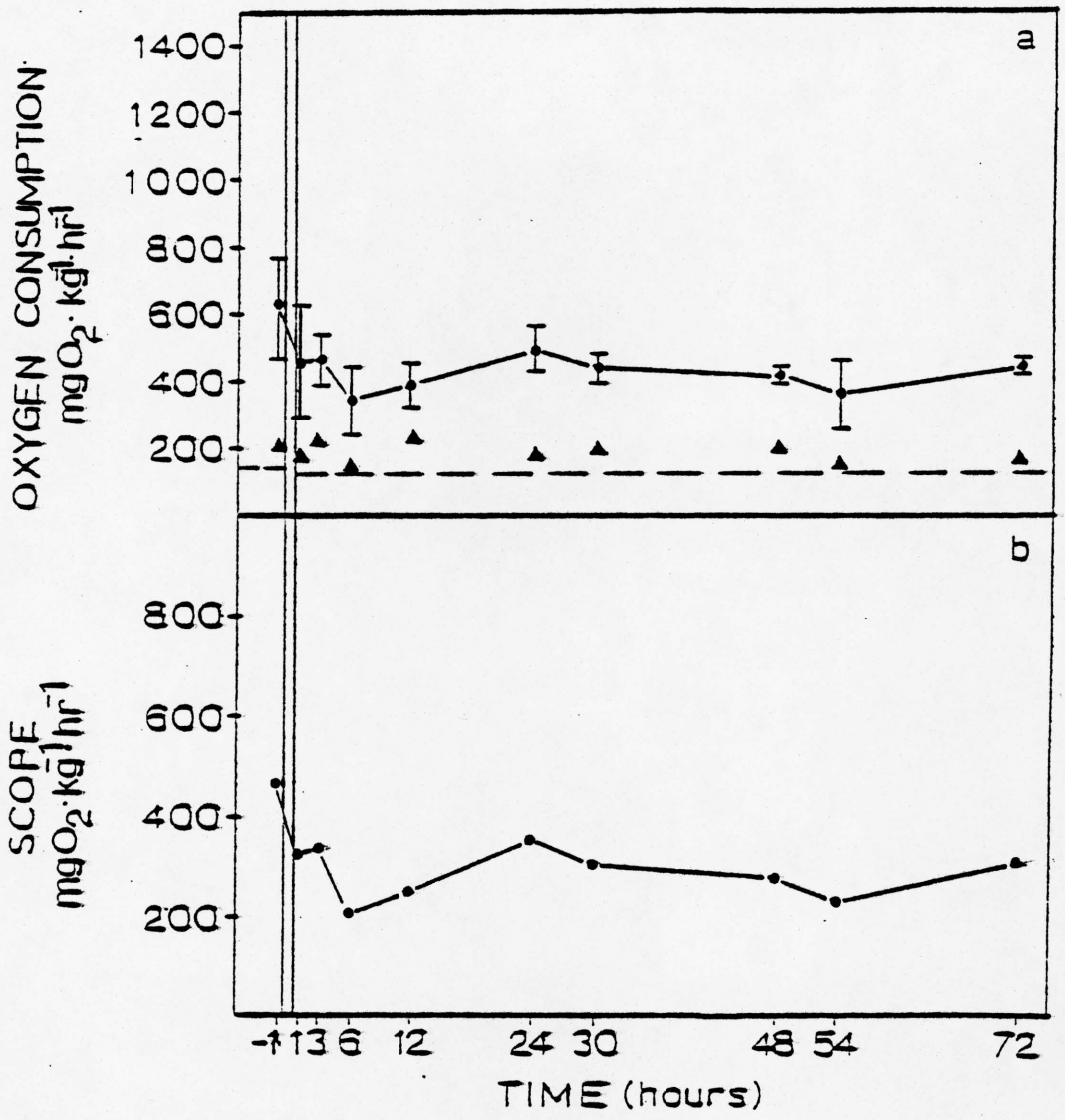


Figure 11. Red drum 15°C, 20-10 ppt.--(a) Time course of ● active (4 TL/s), and ▲ resting (0 TL/s) oxygen consumption following a one hour salinity change from 20 to 10 ppt standardized for a 10 g fish. Dashed line is calculated standard metabolic rate. (b) Time course of ● metabolic scope for activity.

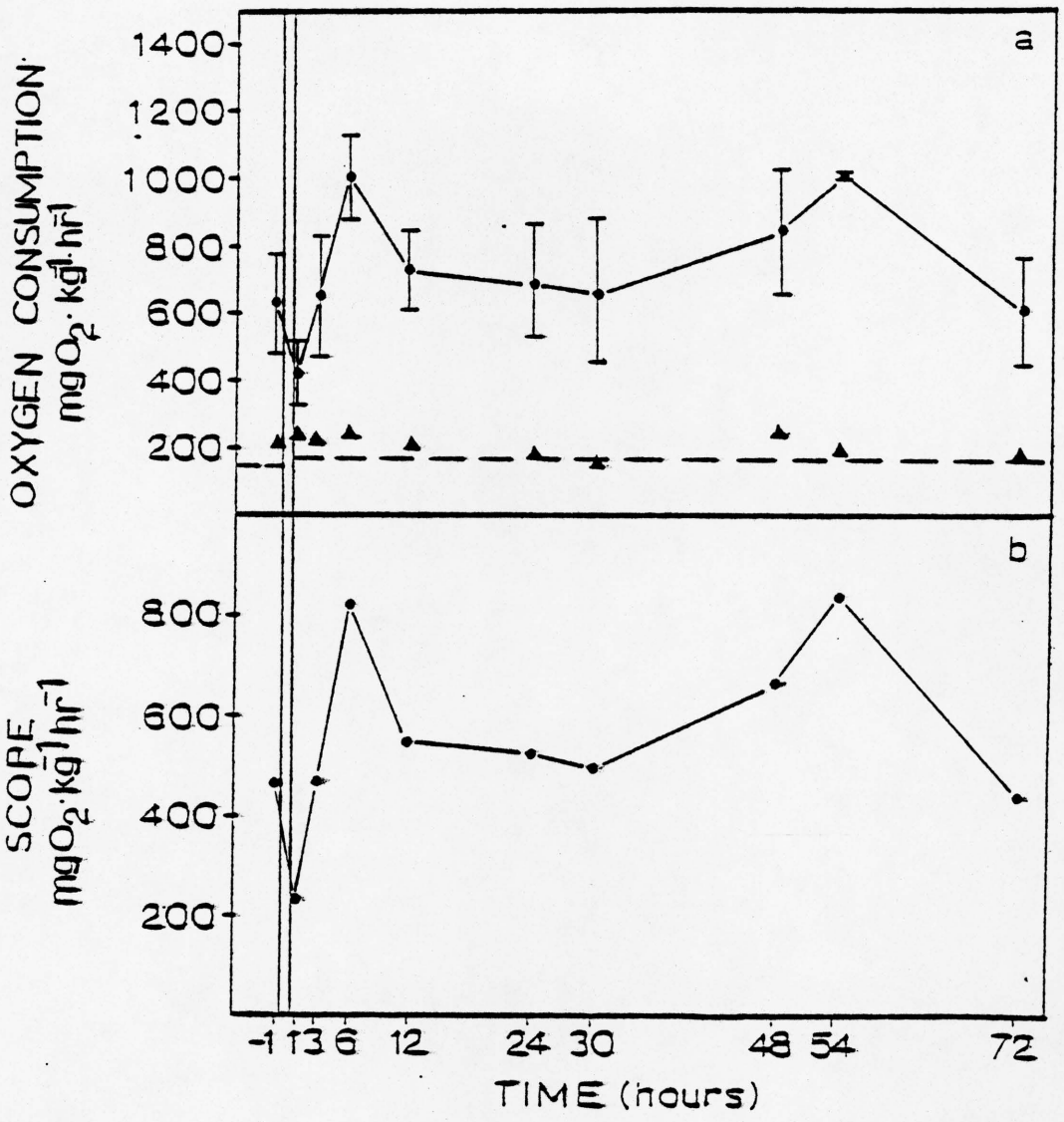


Figure 12. Red drum 15°C, 20-30 ppt.--(a) Time course of ● active (4 TL/s), and ▲ resting (0 TL/s) oxygen consumption following a one hour salinity change from 20 to 30 ppt standardized for a 10 g fish. Dashed line is calculated standard metabolic rate. (b) Time course of ● metabolic scope for activity.

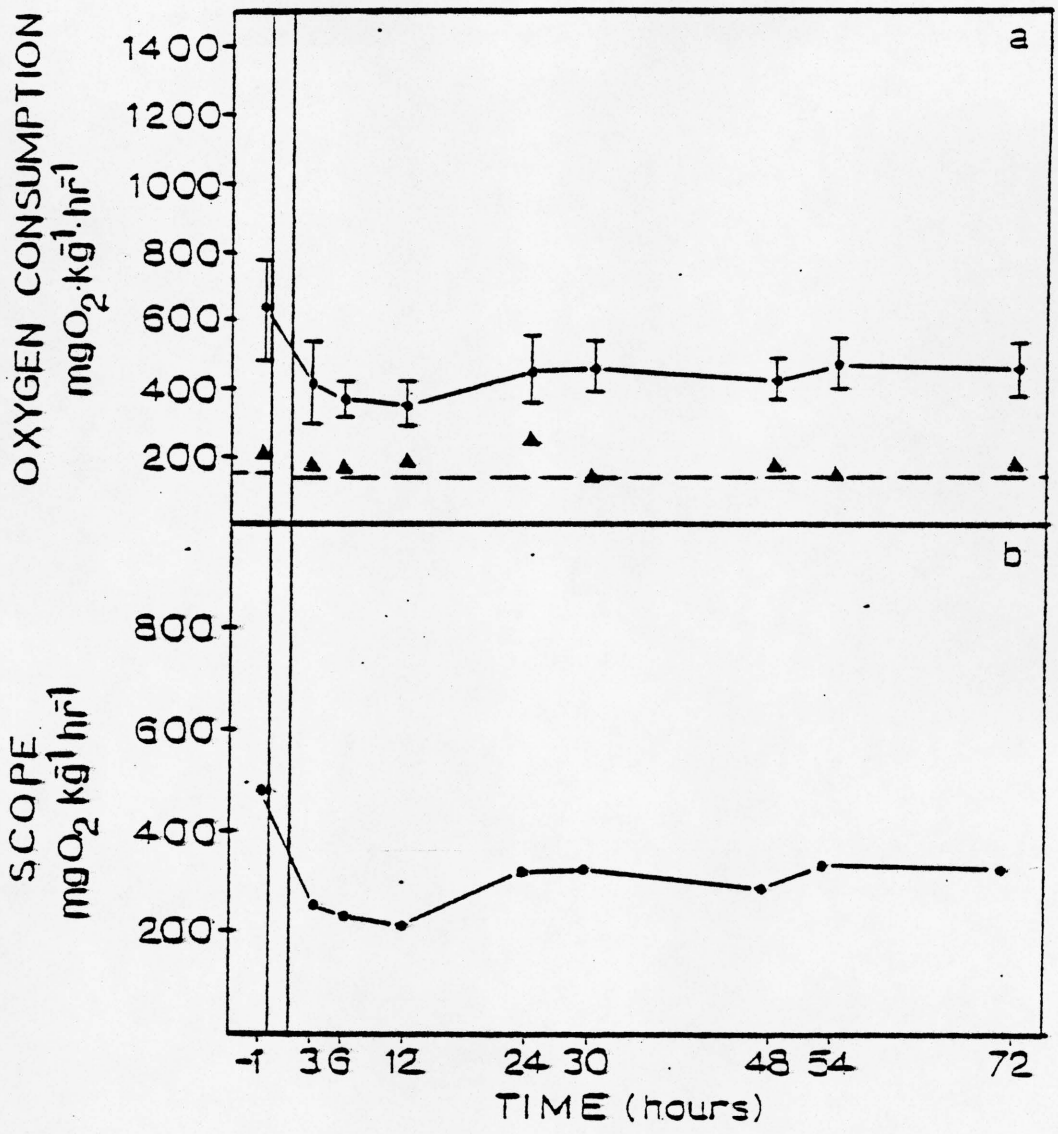


Figure 13. Red drum 15°C, 20-40 ppt.--(a) Time course of ● active (4 TL/s), and ▲ resting (0 TL/s) oxygen consumption following a two hour salinity change from 20 to 40 ppt standardized for a 10 g fish. Dashed line is calculated standard metabolic rate. (b) Time course of ● metabolic scope for activity.

This brief stress period was followed by a rapid increase in maximum active metabolic rate which peaked at 6 hours after the change at both temperatures. Following this peak, the active rate decreased and remained fairly stable during the second day. After 54 hours, however, there is a rise to another peak.

Metabolism and 20-to-10 ppt Salinity Change

Time course plots of metabolism following a change from 20-to-10 ppt exhibit the more typical time course pattern with reaction stressed, recovery and stabilizing phases as described previously. There are minor differences between species and between temperatures (see Figs. 2, 5, 8 and 11.). Although the 28°C time courses appear to have a slower rate of decrease in the active oxygen consumption rate immediately following the salinity decrease, this may be due to the effect of body size rather than temperature. The fish used at 28°C were generally larger than those at 15°C due to normal seasonal growth. In most cases the rate of decrease was slower for the larger fish (see Discussion).

The degree of recovery, however, appears to be dependent upon salinity and temperature. For spotted seatrout, the degree of recovery is greater at 28°C than at 15°C. The red drum data also indicate greater recovery at 28°C.

Metabolism and 20-to-30 ppt Salinity Change

The metabolic responses to this salinity change show striking differences between species and between temperatures.

Spotted seatrout at 28°C show a marked recovery to a higher level of scope at 30 ppt than at 20 ppt. There is also a very high degree of variability in this time course. At 15°C the recovery response was very slow in this experiment, and it is questionable whether or not metabolic rates have been stabilized by the 72-hour termination of the experiments. Comparison of the 72-hour level at 15°C with other data available for this species points to a severe depression of metabolic rate in the present experiment.

For red drum, the response to a 20-30 ppt change is quite unique at both temperatures as mentioned previously. Interpretation of the time course plot may be aided by examining the time course of blood osmolality for a 20-30 ppt change in this species. (See Fig. 14b, discussed later.)

Metabolism and 20-to-40 ppt Salinity Change

The metabolic response to a 20-40 ppt change is almost identical between spotted seatrout and red drum at 15°C (see Figures 7 and 13). The overall level of active metabolism, however, is higher in spotted seatrout. At 28°C (Figure 10) red drum exhibited no recovery phase and suffered greater than 50% mortality after 30 hours. The sequence at 28°C for spotted seatrout (Figure 4) is somewhat erratic. The active rate measurement at 12 hours is thought to be high due to one aberrantly high reading. Spotted seatrout juveniles are clearly more tolerant of increased salinities at high temperatures than red drum.

Blood Osmolality

Whole blood osmolality was measured in small (1-5 g) juvenile red drum at 15 and 28°C. There was no perceptible difference between the two temperatures, however, and the data were pooled for each time interval and summarized in Table 11. The salinity changes to increased salinities both yielded osmolality data which exhibited bimodal frequency distributions at some point during the time course, with the higher mean level about 100 mOsm/kg higher than the lower mean level. Although mortality was not well recorded, there was a higher mortality rate coinciding with the timing of the higher blood osmolality values (see Figure 14a and b). The bimodality could be the result of laboratory diuresis, individual differences, or sexual differences.

Osmolality and 20-to-10 ppt Salinity Change

The 20-10 ppt salinity change is characterized by a very gradual decrease in osmolality over the first 6 hours from 326.7 to a level of about 316 mOsm/kg, followed by a gradual increase over the next six hours (Figure 14c). The time course is generally quite horizontal indicating only very slight perturbation of blood osmolality caused by a 10 ppt reduction in salinity. No bimodality of osmolality measurements was observed. The isosmotic point for juvenile red drum is approximately 10 ppt.

Osmolality and 20-to-30 ppt Salinity Change

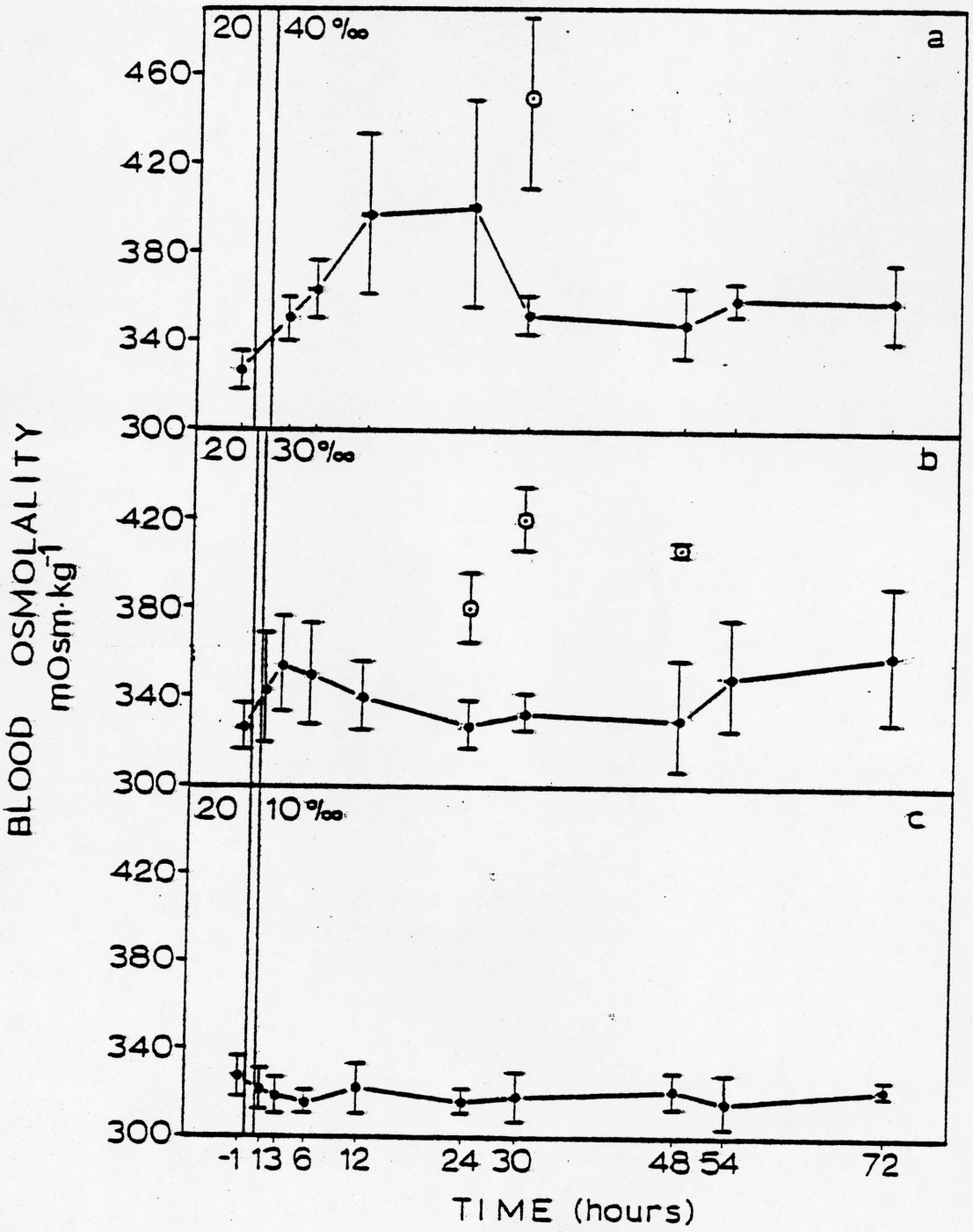
The 20-30 ppt change (Figure 14b) resulted in a rapid

Table 11. Time course of blood osmolality. Red drum.

Salinity Change ppt	Time from Change h	N	Average Blood Osmolality $mOsm \cdot kg^{-1}$	Standard deviation
20-10	-1	27	326.7	9.5
	1	13	320.6	11.2
	3	13	318.7	8.5
	6	13	315.8	5.9
	12	13	322.1	12.2
	24	13	315.9	6.2
	30	13	317.8	12.1
	48	12	320.8	8.3
	54	10	315.3	13.1
	72	13	322.5	5.0
20-30	-1	27	326.7	9.5
	1	6	344.0	26.5
	3	7	354.3	22.4
	5	9	349.2	23.2
	12	8	340.1	15.9
	24	5	327.0	10.9
	24*	3	380.0	16.0
	30	7	332.8	9.3
	30*	2	419.5	14.8
	48	7	329.6	26.5
	48*	2	407.5	3.5
	54	9	350.0	24.9
	72	9	359.0	31.9
20-40	-1	27	326.7	9.5
	3	8	349.4	10.5
	6	12	363.0	13.0
	12	16	396.7	36.4
	24	13	400.0	47.0
	30	7	352.4	7.6
	30*	2	450.0	42.4
	48	7	348.6	15.2
	54	6	359.5	8.3
	72	7	358.1	17.9

*Indicates observed bimodal frequency distribution. Values are of the higher mode.

Figure 14. Time courses of blood osmolality for juvenile red drum following changes from (a) 20 to 40 ppt, (b) 20 to 30 ppt, and (c) 20 to 10 ppt. 15°C and 28°C data are pooled.


20
40‰
a
460
420
380
340
300
20
30‰
b
420
380
340
300
20
10‰
c
420
380
340
300
-1 1 3 6 12 24 30 48 54 72
TIME (hours)
BLOOD OSMOLALITY
mOsm·kg⁻¹

increase in blood osmolality over the first 3 hours to a level of 355 mOsm/kg. This was followed by a gradual decrease over the rest of the first day. At 24 hours after the change, a bimodal frequency distribution of osmolality values appeared which was not attributable to temperature, size, or any known variable. This phenomenon was also apparent at 30 and 48 hours after the change. There were single elevated points at 54 and 72 hours after the change, but the bimodal frequency constraint was not met and these points were lumped with the lower values. Interestingly, between 48 and 72 hours, average blood osmolality increased to the high level observed at 3 hours. Mortality was greatest during the second day of the time course.

Osmolality and 20-to-40 ppt Salinity Change

The salinity change from 20 to 40 ppt, over a two-hour period, caused a rapid increase in blood osmolality over the first 12 hours to a level of about 400 mOsm/kg, which was maintained over the next 12 hours (Figure 14a). At the 30-hour time frame, the mean level was down to about 350 mOsm/kg for 7 out of 9 fish. Two fish had inordinately high values, which met the bimodal frequency constraint, and were given a separate mean and standard deviation. Several fish had elevated values of blood osmolality at 12 and 24 hours after the change, but because of lack of separate modes, these were lumped with the lower values, which resulted in wider standard deviations for these times. Blood osmolality remained steady at around 350 mOsm/kg between 30 and 72 hours. This level is 25 mOsm/kg higher than the

acclimated 20 ppt level of 326.7 mOsm/kg. Mortality following this salinity change was greater than in the 20-30 ppt change and was highest during the first day.

DISCUSSION

General

Emphasis is on relatively rapid adjustments to salinity change and on methods for assessing the accompanying metabolic changes. Therefore this study is relevant indirectly to the usually very slow, natural changes in salinity regimes that occur in Texas coastal estuaries, especially in the case of increasing salinities. Sudden freshening of coastal waters, however, can occur within a day or so following torrential tropical storm-borne rains.

The effects of rapid changes in the osmotic, ionic, and solubility characteristics of the external medium are numerous. In fish, the most obvious and perhaps the most immediately stressful variable is the osmotic pressure exerted upon the epithelial membranes of the gills. Reductions in salinity will cause water to enter the blood by osmosis unless the permeability of the gill epithelia to water is reduced. The permeability of the gill to water is largely controlled by endocrines, notably prolactin (Bern, 1975), and levels of this hormone have been shown to increase in Platichthys stellatus upon transfers from seawater to freshwater (Johnson, et al., 1974). Outflux rates of individual ions, which are controlled by active transport and exchange processes usually involving ATP expenditure, are expected to and have been shown to slow after seawater to freshwater transfers (Motais, et al., 1966; Bern, 1975; Maetz, 1974).

Increases in salinity, on the other hand, would cause excessive water loss and dehydration if mechanisms of water uptake and salt excretion were not well developed in the juvenile fishes involved in this study. Adaptation to increased salinity in teleosts involves an increase in drinking rate coupled with increased salt excretion rates, especially at the gills (Motais, et al., 1966; Kirsch, 1972; Maetz, 1974).

Changes in salinity involve costs to the organism for regulation of transport and metabolic functions, which can change with an altered external environment. The magnitude of these costs on a steady state basis has been studied in fishes previously. The cost of osmoregulation usually increases with the osmotic gradient as salinity increases above the isosmotic point (Rao, 1968; Fry, 1971; Nordlie and Leffler, 1975). However, this should not be taken to mean that the optimal salinity for a species is at its isosmotic point. The metabolic responses to salinity appear to involve more than the cost of osmoregulation alone. Although the standard oxygen consumption rate may be lowest at the isosmotic point, the maximum capacity for activity and the oxygen consumption rate at maximum activity has been shown to occur at salinities higher than the isosmotic point in both species involved in this study (Wakeman and Wohlschlag, 1978; Ilg, 1979). This suggests that the "optimum" salinity may increase with increasing levels of activity for a salinity range of 10 to 30 ppt.

It should be noted here that metabolic scope is a measure of the oxygen consumption capability or capacity which may be used to pay the costs of stress from environmental circumstances. That

point where scope is highest along a gradient of some environmental variable may be considered an optimum in terms of the ability to use oxygen and perform at high levels of activity. This optimum, however, does not necessarily imply that other processes such as assimilation, growth, or reproduction are optimized at that point, although Brett's (1976) summary indicates that thermal optima are nearly identical for many processes.

Another factor which has direct bearing on the above discussion is the effect of body size on the response to acute salinity changes and on the levels of oxygen consumption observed at acclimated conditions of differing salinities. The fundamental basis for the effect of body size is the increased surface/volume ratio of small fish relative to large ones. Small fish have proportionately larger gill surface areas and smaller blood volumes than larger fish, but this fact alone does not directly answer the question of whether small or large fish are stressed more by salinity changes. While the small fish has more relative area which osmotic processes can act upon, they also have a larger regulating surface since the gills are the primary site of ionic regulation. The weight coefficients (b_w) in the multiple regressions on oxygen consumption in Tables 1 and 2 show a decreasing trend with increased salinity. This would point to a higher relative oxygen consumption for small fish than large fish at high salinities. It appears then, that the larger gill surface area of small fish is less beneficial because of increased osmotic pressure than more beneficial because of increased regulatory area.

In order to determine the time course of adaptation to salinity changes of varying degrees and directions, the metabolic data were subjected to a standardization procedure which related the data to a 10 g fish. Since the metabolic rate is largely governed by body size, this procedure was necessary to make the various experiments, which utilized different sizes, directly comparable. Velocity, already standardized by length, ($\overline{TL}\ s^{-1}$), also required further standardization because the active metabolic rate, which is measured at observed maximum velocity, varied within experiments.

The observed maximum sustained velocity is here defined as the highest velocity at which the tail beat of the fish has a regular frequency and above which the fish changes to a burst and glide mode of swimming. This definition works well for single, large fish, but when over 30 juveniles are in the chamber, a certain amount of subjectivity is induced. Because of this problem, all active data were standardized for a 10 g fish swimming at 4 $\overline{TL}\ s^{-1}$ using multiple regressions from Tables 1 and 2. The only basic problem with this procedure is that it ignores the probable interaction of the variables of weight and velocity.

Fortunately, only relatively small weight and activity ranges are involved in these standardizing procedures for 10 g and 4 $\overline{TL}\ s^{-1}$, but for larger size and activity ranges a separate study of weight and velocity interactions would be required.

The resting oxygen consumption rate at 28°C is elevated far above the estimate of standard metabolism for this temperature, which is probably due to spontaneous and uncontrolled physical

activity by the fish at this temperature. Field collected red drum during the summer were too large to use in the flasks, so usually smaller juveniles which were obtained from the Texas Parks and Wildlife Department were used for resting measurements. Since measurements of the resting rate took place in sealed 2.9 l flasks, the smaller the fish, the less restrictions on its movement. The fact that 28°C is far above the temperatures normally experienced in winter and spring by small juveniles may be an important factor as well!

Uncontrolled and unmeasured activity is a major drawback for the use of the "resting" metabolic rate as an indicator for any purpose. For this reason, calculations of metabolic scope utilized the estimate of the standard metabolic rate from the regressions in Tables 1 and 2, rather than measured values of the "resting" metabolic rate. This procedure assumes that the standard rate is constant after the salinity change. While this assumption is not absolutely true, changes in the standard rate are usually very small relative to those in the active rate, so that the estimate of scope is only slightly affected by the assumption. The observed, small changes in the resting rate tend to support this procedure. Since variations in the active metabolic rate are much greater than those observed in oxygen consumption at low levels of activity, the magnitude metabolic scope is much more arithmetically dependent on the active metabolic rate. Because of this direct correlation, the analyses on the time courses which follow deal directly with the active metabolic rate, although it should be noted that the same relationships generally hold for metabolic scope.

Metabolic Responses

The general shape of the time course of metabolic responses was described in the results section. For purposes of discussion, the various phases of an idealized time course are labeled in Figure 15. The majority of the time courses in Figures 2-13 seem to lend themselves to this division. The observed decrease in the active metabolic rate following the salinity change is, in itself, interesting in view of the fact that performance (velocity) did not decrease proportionately as would be expected (see Tables 7-10). The efficiency of swimming superficially appears to increase during this period, which is highly questionable and indeed unlikely. A second explanation could involve a large increase in the anaerobic component of metabolism. A sustained anaerobic component of this magnitude, however, must be viewed with a great deal of skepticism, because the muscle fibers involved in glycolysis are not adapted for swimming activity on a sustained basis (Goldspink, 1977; Bilinski, 1974). Perhaps the best explanation, therefore, involves the possibility of a reduced energy allocation to such energy demanding processes as anabolic metabolism. A temporary reduction in the processes of growth and synthesis may be the price paid for the costs of adaptation to salinity changes when activity, growth, and ion-osmoregulation compete for energy.

The direction or degree of salinity changes has surprisingly little effect on the rate of short term metabolic adaptation. In the majority of cases, a large degree of recovery and possible stabilization has occurred by 30 hours. Since the level of

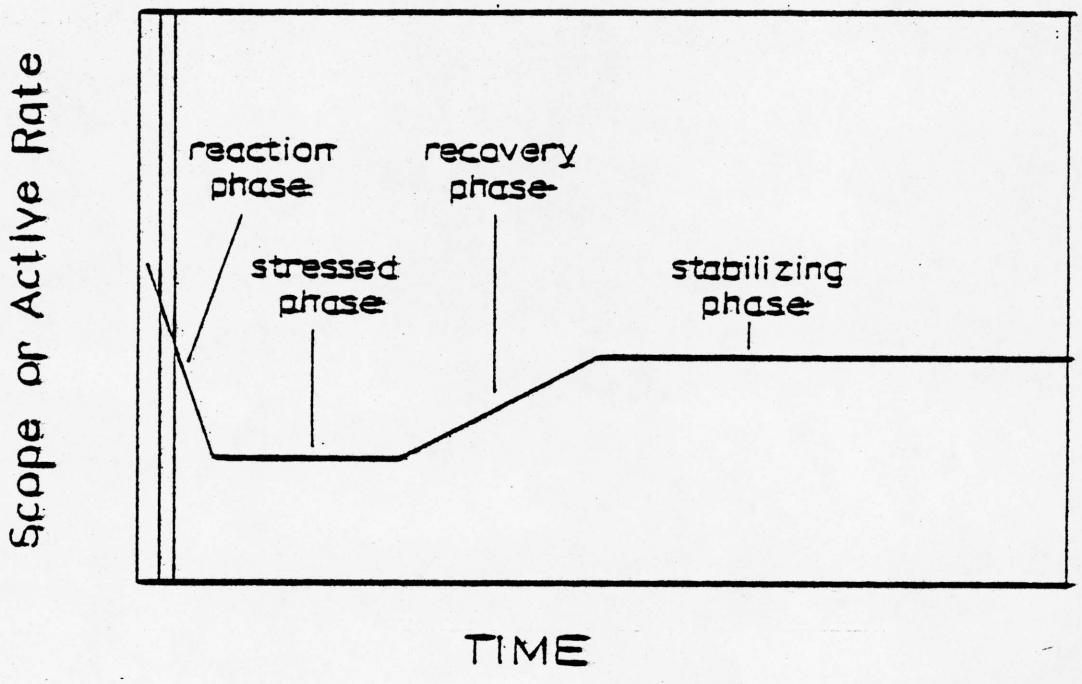


Figure 15. Idealized time course of metabolic scope or the active metabolic rate, denoting the various phases in the adaptation process.

stabilization is usually reached in about 30 hours, the rate of decrease during the reaction phase, the duration of the stressed phase, and the level of the stabilization phase remain as possible responses which may be governed by size, salinity, temperature, or species differences.

The rate of decrease during the reaction phase is largely governed by size. In Figure 16, the average decrease in the active metabolic rate during the first 3 hours after a salinity increase is plotted as a function of weight. This relationship shows that for small juveniles at 20 ppt (< 25 g), the effect of salinity increases to 30 or 40 ppt is responded to more rapidly by the smaller individuals. The same function does not apply to salinity decreases or to juveniles weighing more than 25 g. The response of larger juveniles was more rapid than what would be predicted by extrapolation of the function observed for small juveniles.

The duration of the stressed phase of the time course seems to be a function of salinity in the red drum. Figure 17 shows the average duration of the condition of reduced active metabolic rate as a function of final salinity in this species. As expected, the duration is shortest for the 20-30 ppt change. By this measure, the 20-40 ppt change is the most stressful and the 20-10 ppt change is intermediate. There was no clear relationship between duration of the stressed phase and body size, but a large number of the time courses using small juveniles began the recovery phase immediately after the reaction phase resulting in no easily measurable stressed phase. This was the general case

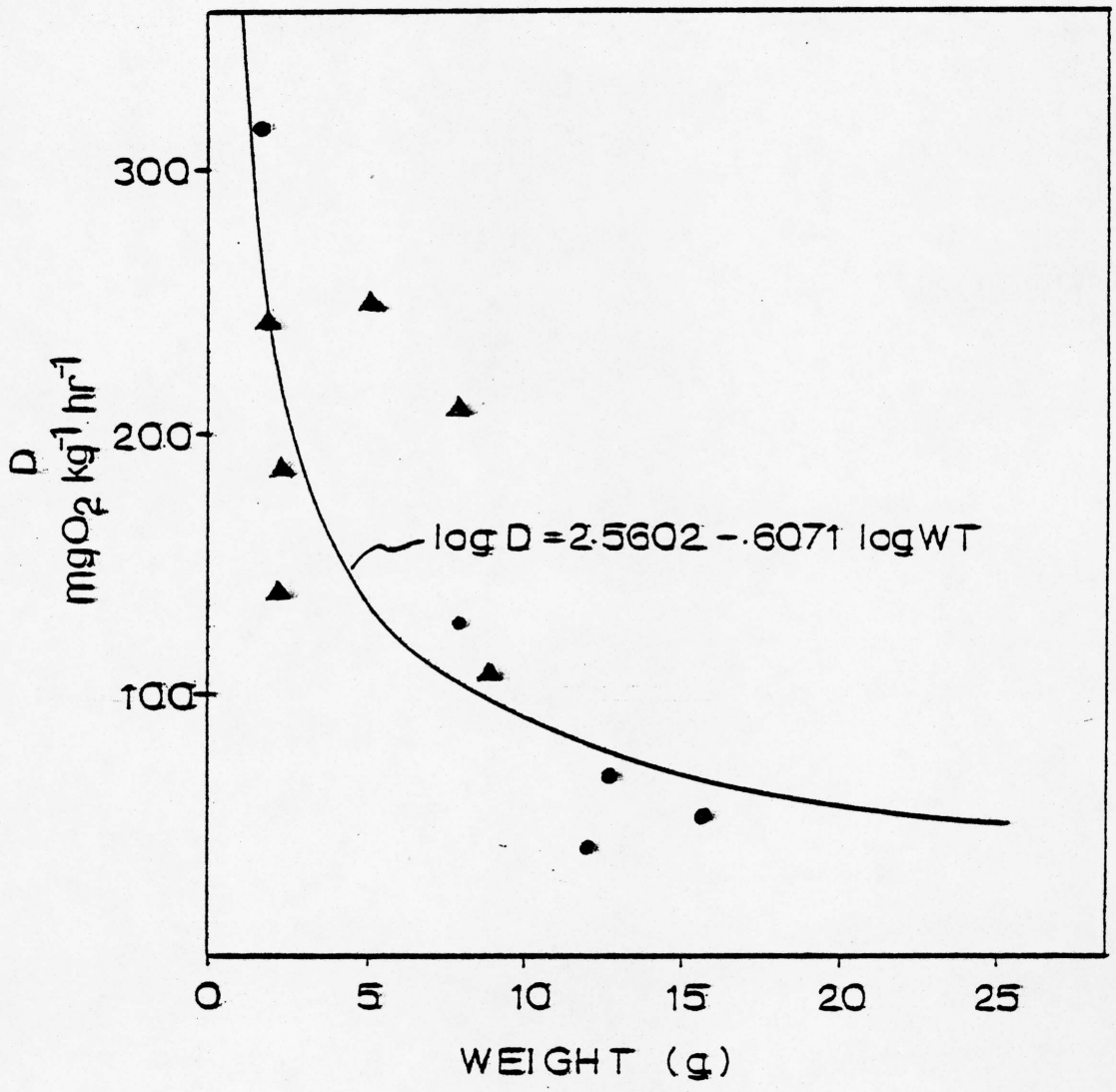


Figure 16. Average decrease (D) in the active oxygen consumption rate of juvenile red drum during the first three hours following salinity increases to ● 30 ppt and ▲ 40 ppt.

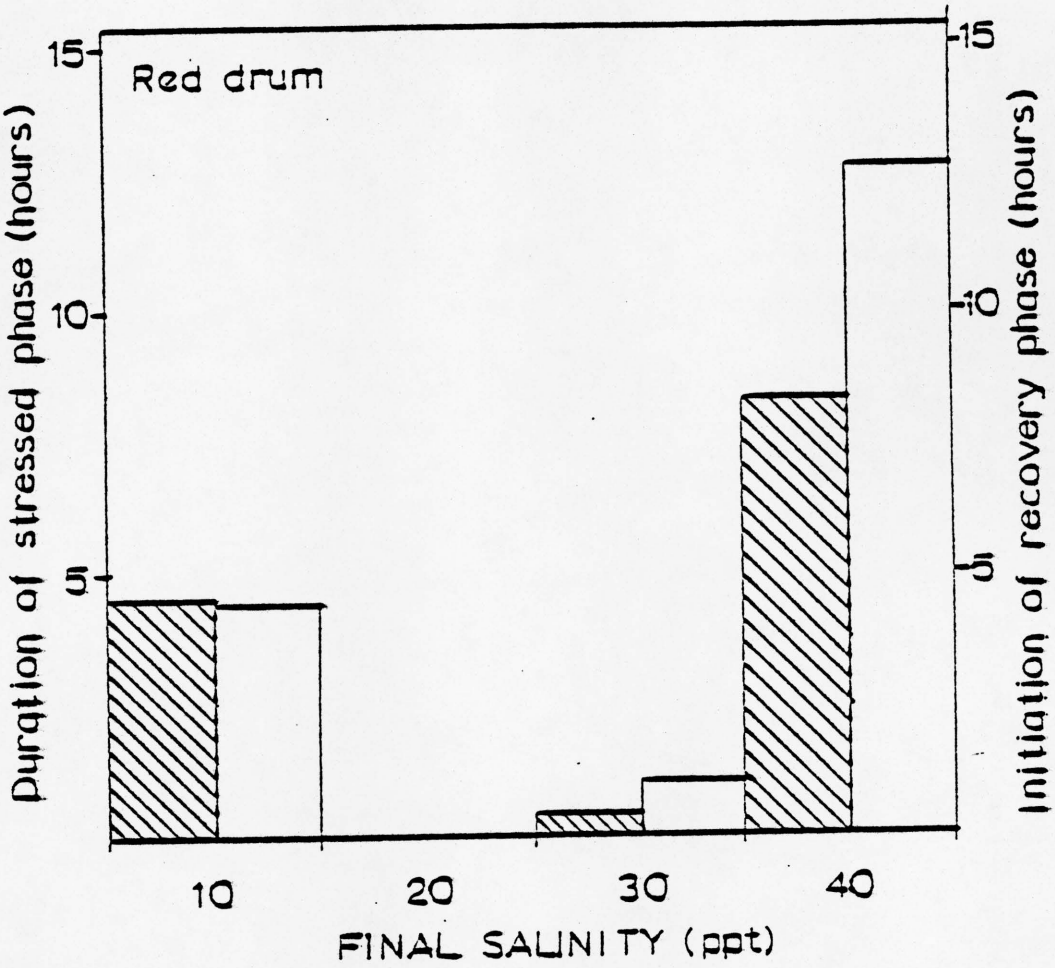


Figure 17. Histogram showing the relationship of ▨ the duration of the stressed phase, and ▭ the time of initiation of the recovery phase to salinity in juvenile red drum.

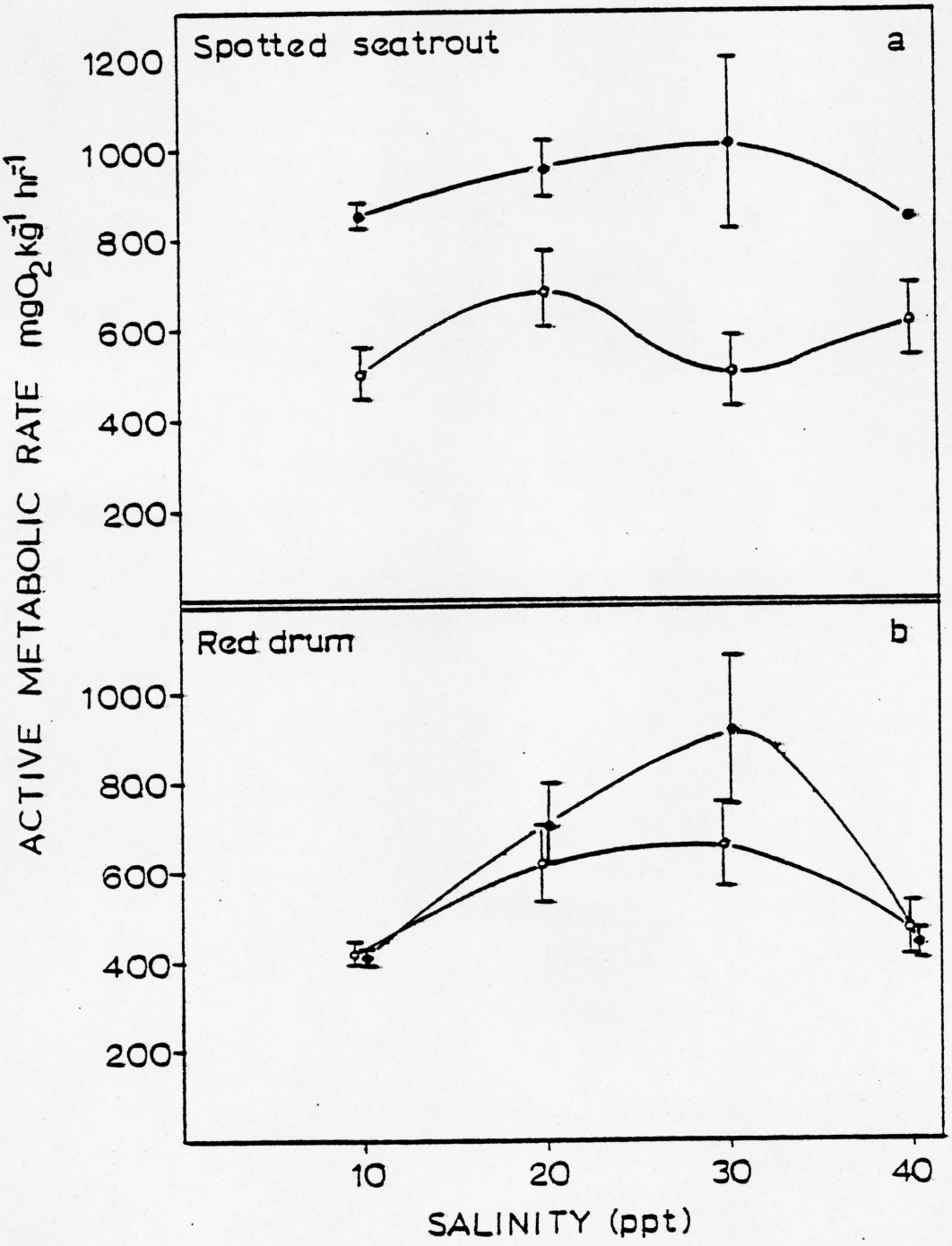
for 20-30 ppt changes in red drum. Spotted seatrout showed no such discernable trends.

The time of initiation of the recovery phase shows a very weak positive correlation with body size over the small (< 25 g) size range. Again, salinity appears to be the primary factor governing the rapidity of recovery, at least in red drum (see Figure 17). The weak correlation with size suggests, however, that small juveniles may be more resilient to sublethal salinity stress even though increased salinity affects them more, due to surface-volume considerations.

The level of the stabilization phase is clearly a function of salinity as shown in Figure 18. While the data here are probably insufficient to predict the salinity optima, the basic shape and position of these relationships agree with previous data (Wohlschlag, 1977). The depressed value of the active metabolic rate of the spotted seatrout at 15°C, 30 ppt, is probably a result of stress from trawl capture as discussed below. Since by definition a fasted condition is necessary for the metabolic determinations in this experiment, an effect of starvation may cause a slight reduction in the level of stabilization by the end of 3 days. For this reason, the level of stabilization as depicted in Figure 18 should not be over-emphasized.

In relation to salinity changes, the effect of temperature was most apparent in juvenile red drum in changes from 20 to 40 ppt. The fish showed a typical response and recovered at 15°C but suffered mortality and did not recover at 28°C. The mortality

Figure 18. Active metabolic rates at 72 hours after the salinity change versus final salinity at ● 28°C and o 15°C, for spotted seatrout and red drum.


Spotted seatrout
a
Red drum
b
ACTIVE METABOLIC RATE $mgO_2kg^{-1}hr^{-1}$
1200
1000
800
600
400
200
1000
800
600
400
200
10
20
30
40
SALINITY (ppt)

may have been associated with the fact that 28°C is fairly close to the upper lethal temperature for red drum (approx. 32°C). Fish show different responses to the upper lethal temperature than to the lower, death being more abrupt at high temperature and less so at low temperature.(Fry, 1957). Another factor which is almost certainly important in this case is that one of the experiments involved unseasonably small (1-2 g) juveniles obtained from the Texas Parks and Wildlife Department. Juveniles of this size are probably seldom exposed to high salinities at temperatures as high as 28°C, because they reach this size in the winter months and by summer are considerably larger. Yokel (1966) reported a direct relationship between size and salinity for this species: he noted that small fish are more common at low salinity and large fish are more abundant at higher salinities.

Spotted seatrout juveniles appear to be more tolerant of increased salinities at 28°C. The optimal spawning temperature for this species is 28°C (Taniguchi, in press; Weaver and Perret, 1979), so the high temperature is not expected to be a stressing factor for these juveniles.

In spotted seatrout, at 28°C (Fig. 3), the change from 20 to 30 ppt resulted in a higher stabilized active metabolic rate at 30 ppt than at 20 ppt. At 15°C, however, the recovery phase was very gradual and resulted in a lower active rate at 30 ppt than at 20 ppt. The only difference noted in the 15°C experiment is that the fish were captured by otter trawl. This method of capture causes more damage to skin and scales.

The observed response to salinity changes from 20 to 30 ppt in red drum (Figs. 9, 12) deserves mention. The pattern observed

at both temperatures differs markedly from the pattern observed at all other salinity changes and from that of the spotted seatrout. The fact that the change is toward the optimum salinity probably has some pertinence. If the fish's physiology is regulated such that it is capable of greater oxygen consumption at 30 ppt, it is not implausible that an overshoot and subsequent compensation could account for the first peak at 6 hours. As for the second peak, blood osmolality (Fig. 14) is observed to begin a second increase at 48 hours. This could elicit a metabolic response, but one would expect it to be a negative one rather than the observed peak in the active metabolic rate at 54 hours. For the present, random variability or some type of behavioral manifestation is perhaps the best explanation.

Blood Osmolality

The observed changes in blood osmolality (Fig. 14) following the experimental salinity changes for red drum show a general correlation with the metabolic responses. By 30 hours, a degree of stability is observed in all three cases. The perturbations in osmolality agree both in direction and degree with changes in the external salt concentration. The elevated values observed following salinity increases are possibly the result of laboratory diuresis (Kinne, 1962). Since the salinity history of the fishes is unknown, however, these may represent a case of irreversible nongenetic adaptation (Kinne, 1962). If the juveniles in question were spawned at low salinity, their adaptational response to increased salinity may be impaired.

The 72-hour level of blood osmolality is considerably higher at both 30 and 40 ppt than at 20 ppt. This observation was also noted in a separate experiment where juvenile redfish were allowed to adapt for 14 days. The implications of this difference are that every cell in the organism must adjust to a new internal milieu. This could be the basis for the observed salinity optima between 20 and 30 ppt for red drum.

The fact that temperature had no apparent effect on blood osmolality is contrary to that observed for Fundulus heteroclitus (Umminger, 1968). This species showed higher concentrations of Na^+ and Cl^- in winter than in summer. Prosser, et al. (1970) suggest that this could have energy saving properties by reducing the osmotic gradient when energy supply is low in the winter. There are actually too few data points to determine statistically the effect of temperature on blood osmolality in this experiment, so this question should not be considered answered.

At 30 ppt, blood osmolality (Fig. 14) shows a second increasing trend beginning two days after the salinity change. Associated increases in the standard deviation of the means are also apparent. The physiological basis for this increase is unknown, but starvation, periodicity, a real pattern of regulation, or random variability are all possible explanations.

The very slight perturbation of blood osmolality in 20-10 ppt changes is interesting in that it suggests that these small juveniles adapt to rapid salinity decreases faster than to salinity increases. In view of the fact that rapid salinity decreases in the estuaries due to heavy rainfall and rapid runoff are much

more common than rapid increases due to evaporation, this result is expected. Potts (1954), on theoretical grounds, has shown that the energy expenditure involved in regulation to dilution of the medium is less demanding than regulating for increased concentration.

CONCLUSIONS

1. Initial metabolic responses of juvenile (less than 25 g) spotted seatrout and red drum, which had been acclimated to an optimal salinity of 20 ppt and then subjected to a reduction to 10 ppt or increases to 30 or 40 ppt, were:
    a. The active metabolic rate was reduced substantially.
    b. The scope for activity was reduced substantially.
    c. The standard metabolic rate changed relatively only slightly.
2. Following the salinity increase or decrease the active rate and scope decreases briefly during a "reaction" phase.
3. The initial active metabolic rate decrease is either followed by an immediate gradual increase in the active rate in a "recovery" phase or followed by a continued relatively low metabolic state termed a "stressed" phase. The stressed phase was always present for salinity changes from 20 to 10, and from 20 to 40, ppt and was followed either by death or a recovery phase.
4. Changes from 20 to 30 ppt were not necessarily stressful.
5. Following the recovery phase, the active metabolic rate tends to level off in a "stabilizing" phase.
6. The stabilizing phase is usually at a lower level for both active metabolism and for scope than the initial levels at 20 ppt, except for the changes to 30 ppt. Usually the stabilizing phase began about 30 hours after the salinity change.
7. Smaller juveniles show a faster rate of decrease in active metabolic rates during the reaction phase and an earlier recovery

phase. The explanation is suggested by the relative changes in the gill surface-to-volume ratios with growth.

8. Since a large degree of metabolic stabilization has occurred by 30 hours after salinity changes from an acclimated 20 ppt to 10, 30, or 40 ppt, it is conservatively estimated that short term salinity acclimatization occurs in about 48 hours, except for a few deaths.

9. The duration of the stressed phase for red drum is apparently related directly to the amount of salinity increase above 20 ppt, while a decrease to 10 ppt had a stressed phase of intermediate duration.

10. The time from the salinity change to the beginning of the recovery phase was generally shorter for the smaller of the red drum juveniles.

11. The level of stabilization in the active metabolic rate or in the scope level was a direct function of salinity, both with optima between 20 and 30 ppt, as indicated for larger specimens in earlier studies.

12. Except where temperatures are comparatively high, the effect of temperature on the salinity acclimation processes is apparently not great. Normal seasonal times of hatching, growth, and temperatures should be taken into consideration concomitantly in salinity change evaluations.

13. The observed changes in blood osmolality following salinity changes tend to follow both the degree of salinity change and the changes in metabolic responses. However, a fair proportion of individuals seemed unable to regulate for salinity increases

to 30 and 40 ppt and suffered mortality. This inability to regulate could be explained by laboratory diuresis or by too rapid exposure to too great a salinity change.

14. The general application of small fish to evaluate rapid changes from ideal estuarine salinity conditions to salinities that may be less than optimal seems to be a worthwhile analytical approach for future fishery resource assessments. The general subtleties observed in this study should be used as a basis of precautions in future applications, however.

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